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LAND BIRDS OF GUADALCANAL AND THE SAN CRISTOVAL GROUP, EASTERN SOLOMON ISLANDS

IAN C. J. GALBRAITH and EBBA H. GALBRAITH

9 OCT 62

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LAND BIRDS OF GUADALCANAL AND THE SAN CRISTOVAL GROUP, EASTERN SOLOMON ISLANDS

IAN C. J. GALBRAITH AND EBBA H. GALBRAITH

SYNOPSIS

A collection from Guadalcanal, San Cristoval and Ugi is reported upon, with systematic and distributional notes covering also the land and freshwater forms not collected. A new subspecies of *Halcyon chloris* is described from the Three Sisters group; a recently-described race of *Tyto alba* is synonymized; changes of arrangement, affecting the nomenclature of forms currently placed in *Coracina tenuirostris, Monarcha barbatus, Myiagra ferrocyanea* and *Myzomela nigrita,* are suggested; and the application of the the names *Pachycephala pectoralis* and *Zosterops rendovae* is discussed.

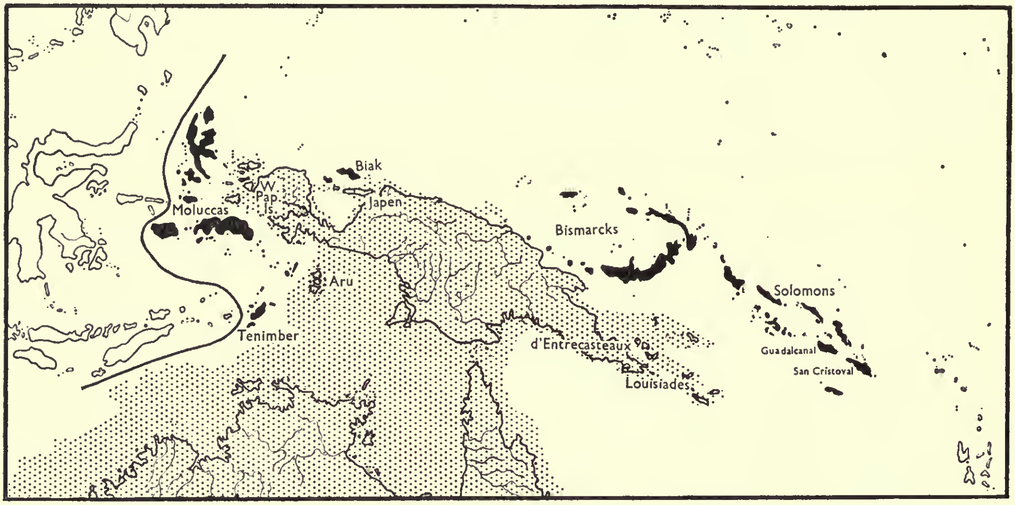
INTRODUCTION

THIS paper is primarily a report on the collection of bird-skins made by the Oxford University (Department of Zoology) Expedition to the Solomon Islands in 1953; but is expanded to cover islands in the San Cristoval group not visited by the expedition, and land and freshwater forms unrepresented in the collection. New subspecies discovered in the mountains of Guadalcanal have already been described (Cain & Galbraith, 1955), while new distributional information and a few taxonomic notes have been given incidentally (Cain & Galbraith, 1956). The expedition, financed mainly by the Percy Sladen Trustees and the Parliamentary Grants Committee of the Royal Society, was led by Dr. A. J. Cain, supported by I. C. J. G. and by native assistants from the Malanggo district of Guadalcanal and the Ravo district of San Cristoval. Almost all the linear measurements presented here were taken by E. H. G., while I. C. J. G. is responsible for the rest of the paper.

Avifaunal Geography

A study of the Solomons avifauna, with special emphasis on the geographical variation for which it is remarkable, is in preparation by I. C. J. G., and only the barest outline will be given here. Grover gives geographical and general accounts (1955: 3–26; 1957; 1958: 3–10), and much detailed geological information with valuable general references (1955; 1958; 1960), for the British Protectorate. Nissan, Buka and Bougainville, with the Bismarck Archipelago, belong politically to the Territory of Papua and New Guinea (see Australia 1950–1951). The area is shown to a convenient scale, and all but the smallest islands named, in the new *Times Atlas* (1958, pl. 15). Apart from minor differences in spelling, only the following names used here for islands in the Solomons are not to be found in the Atlas: Buena Vista = Vatilau; Gower = Ndai; Murray = Buraku; Ranongga = Ganongga; San Jorge = St. George; Sikaiana = Stewart; Simbo, five miles south of Ranongga; Small Malaita = Maramasike.

The Solomons form the easternmost extension of a zone of islands round the western, northern, and eastern coasts of New Guinea, beyond the continental shelf but accessible by island-hopping across gaps of less than two hundred miles (mainly less than eighty). The avifaunas of these islands—the Tenimber and Kei groups, the Moluccas, Biak and Numfor, and the Bismarcks and Solomons—place them in the Papuan region, and have clearly been derived mainly from New Guinea by colonization across the sea. The Moluccas have a considerable Malaysian component, and the Solomons a smaller Polynesian one. Enclosed by this " Molucco-Melanesian " zone is that of the islands on the Papuan continental shelf—Aru, the Western Papuan Islands, Japen, and less certainly the d'Entrecasteaux and Louisiades—with richer faunas perhaps largely derived by direct colonization at periods of lower sea-level, yet lacking many birds characteristic of the mainland. Further out, Micronesia to the north and Southern Melanesia (including the Santa Cruz group and New Hebrides) to the southeast, form a zone with the much poorer faunas characteristic of the Polynesian Region (Mayr, 1941*b*). All three zones are avifaunally characterized not merely quantitatively but qualitatively; though even the continental islands can have had land connections with one another only through mainland New Guinea. The remarkable avifaunal resemblances, in the representation or otherwise of Papuan stocks, between (say) Biak and the Solomons, thirteen hundred miles apart, must be almost wholly due to the different colonizing potentials of the various stocks, across similar barriers and into ecologically similar habitats.



Map 1. The Papuan region, showing islands of the " Molucco-Melanesian " zone (black), in relation to the Papuan continental shelf (stippled to the 200-metre isobath, from B.H.I. 1942), Weber's Line of faunal balance (from Mayr, 1944*d*), and the wider water-gaps of the Polynesian region.

Within the middle zone, the Bismarcks and Solomons together form a rather homogeneous unit, distinguished as Northern Melanesia (Mayr, 1941*b*). As might be expected, avifaunas progressively poorer in species are encountered in passing from the Huon Peninsula of New Guinea, through New Britain and New Ireland to the Solomons. The geography of the area suggests this as the most important colonization route, while some direct evidence for it in the patterns of distribution and variation of some (apparently rather recent) arrivals is not convincingly paralleled for the possible route to the Solomons through the Louisiades. However, the faunal parallelism characteristic of the three zones is shown within Northern Melanesia also. In many stocks, the representative populations in the Solomons are more distinct and diverse, and thus probably older, than those in the Bismarcks. The striking endemism of the Solomons avifauna is exemplified by *Haliaeetus*. *H. leucogaster* occurs, without appreciable geographical variation, from India to Australia, New Guinea and the Bismarcks ; but is represented in the Solomons by the very distinct *H. sanfordi*.

Though a fairly compact and homogeneous archipelago—seven hundred and twenty miles across, with no water gaps of much more than fifty miles, and mostly covered by tropical rain forest—the Solomons proper show considerable avifaunal diversity, in both the representation and the geographical variation of species and superspecies. The most striking discontinuity is met in crossing the thirty-five mile strait from Guadalcanal to San Cristoval : no fewer than 29 of about 95 breeding species are unrepresented, including such widespread and common birds as *Accipiter novaehollandiae*, *Ptilinopus superbus*, *Coracina papuensis*, *Aplonis cantoroides*, *Mino dumontii* and *Nectarinia jugularis*. The internal richness in geographical variation is still more striking : perhaps in no other archipelago does such a high proportion of the avifauna break up into so many and so diverse representatives across such narrow barriers. The most celebrated example is the *Zosterops kulambangrae* (=*rendovae*) superspecies in the New Georgia or Central Solomons group (see Mayr, 1942 : 227—in which the narrowness of the straits is exaggerated—and Mees, 1961 : 143–151). The discontinuities and affinities are not geographically random but express themselves in a rather clear-cut pattern, which may be formalized in a system of avifaunal districts and sections (Mayr, 1945*a* : 275—expanded from Rothschild & Hartert, 1905 : 244). This system is reproduced here with only minor emendations, though a modified form is in preparation. The possibilities of confusion in the avifaunally misleading term " Central Solomon Islands" have been pointed out (Cain & Galbraith, 1956 : 102), and it has since been adopted in yet another sense (Grover, 1957 ; 1958). Here it is replaced by " New Georgia Group ", as used by Grover and the *Times Atlas* (1958). Names and spellings in this paper are as far as possible those officially current in the Protectorate.

A. Main Chain

a. Northern Islands—(Buka), Bougainville, Shortland Is., (Fauro), Choiseul, (Robroy, Wagina, Gagi, Barola, Baroraite), Ysabel, (San Jorge)
b. Guadalcanal Group—Florida Is., (Savo), Guadalcanal
c. Russell Is.
d. Malaita Group—Malaita, (Small Malaita), ? Ulawa

B. New Georgia Group
  - *a.* Western Section—Vella Lavella, (Ranongga), ? Simbo
  - *b.* Main Section—Gizo, Kolombangara, (Wanawana, Arundel), New Georgia, (Vangunu, Gatukai)
  - *c.* Rendova Section—Rendova, (Tetipari)

C. San Cristoval Group—San Cristoval, Ugi, (Bio), Three Sisters Is., Santa Ana, (Santa Catalina)

Parentheses indicate small or moderate-sized islands, lying close to the groups with which they are associated, for which avifaunal lists are not available. Unpublished distributional information from the Whitney Expedition was no doubt used by Mayr (1945*a*) in associating some of them with districts and sections. Smaller offshore islands probably resemble the more isolated ones—Nissan, Treasury, Murray, Buena Vista, Ramos, Gower, Sikaiana and Ongtong Java ; and perhaps Simbo (Sibley, 1951 : 83) and Ulawa (Cain & Galbraith, 1956 : 104)—in having such depleted avifaunas, composed almost entirely of widespread forms, that they cannot be associated faunally with any particular subdivision of the Solomons (nor indeed with one another, within the unity imposed by the ecologically-limited range of potential colonists).

Rennell, with Bellona, has a very distinct avifauna, somewhat intermediate in its affinities between Northern and Southern Melanesia (Mayr, 1931*c* ; Bradley & Wolff, 1956 ; Braestrup, 1956), while the Santa Cruz group is associated with the Solomons only politically, and has a largely Southern Melanesian avifauna.

Within the Solomons proper, the most fundamental cleavage is between the Main Chain and New Georgia Group on the one hand, and the San Cristoval Group on the other. Failure of almost a third of Guadalcanal species to colonize San Cristoval has already been mentioned ; while of 67 San Cristoval species whose distribution is sufficiently known, 17 are represented on Guadalcanal by different (mostly very distinct) subspecies, 5 by different species, and 7 are not represented. Between Guadalcanal and San Cristoval there is a major break in the southeastwards spread of Papuan birds, comparable to that between the Bismarcks and Solomons, and a lesser one in the northwestwards spread of Polynesian forms. Although evident in Mayr's (1945*a*) summary of the Solomons avifauna, this striking discontinuity has not been especially remarked ; largely because most of the San Cristoval endemics were discovered early and only gradually localized within the Solomons, while the absence of otherwise characteristic species has also been only slowly recognized. Ugi and the other small islands have reduced but distinctively San Cristoval avifaunas, with some specialization. The presence of *Aplonis cantoroides* and *Nectarinia jugularis* on these islands, though not on San Cristoval itself, supports other evidence in suggesting that the latter is not an avifaunal vacuum preserved by physical isolation ; but that the endemic forms have redeployed ecologically to form a thin but harmonious avifauna which presents an effective barrier to colonization. This in turn suggests that the island may have had a distinctive history as a terrestrial biotope during the Caenozoic—which the bathygraphy, relief, stratigraphy and tectonics of the Solomons (Grover, 1955 ; 1958 ; 1960) do not contradict.

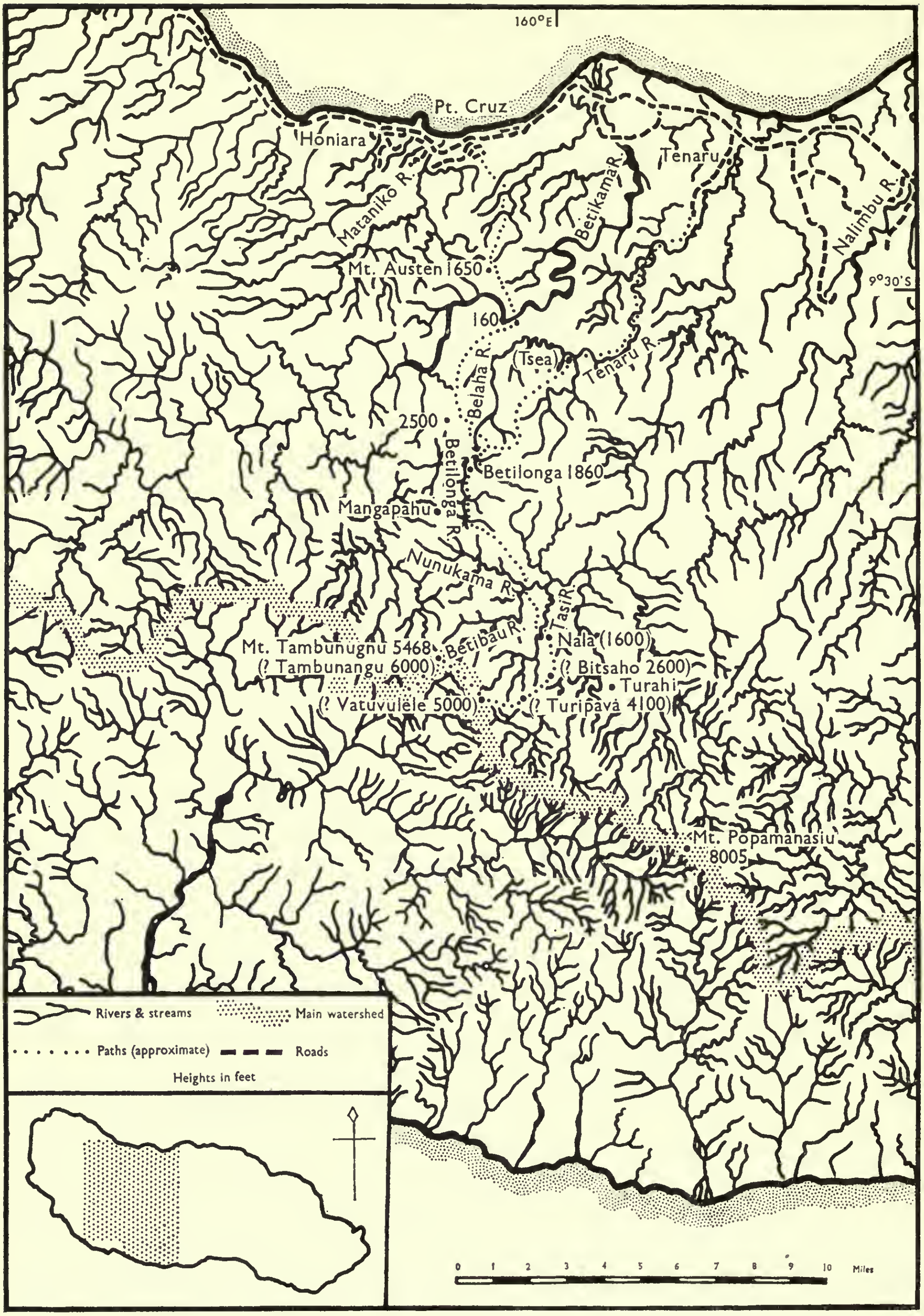
Whereas the San Cristoval forms *Coracina salomonis*, *Monarcha vidua* and *Myiagra cervinicauda* have recently been regarded as conspecific with their representatives elsewhere in the Solomons (Mayr, 1945*a* ; 1955), we treat them as full species. Some of Mayr's species-arrangements of allopatric forms are too much influenced by geography rather than characters, and so may be misleading when faunal affinities are to be considered. Possibly we have fallen into the opposite error through over-preoccupation with the peculiarity of San Cristoval. However, other recent authors have divided some of Mayr's (1945*a*) polytypic species on similar grounds (e.g. Mayr, 1955 : 23 ; Amadon, 1956 : 23 ; Mees, 1961 : 132).

Avifaunal differences between and within the Main Chain and New Georgia Group are much less profound than those which separate the San Cristoval Group. Bougainville and Guadalcanal, the largest and most massive islands, have the richest and most typical avifaunas, with surprisingly little differentiation between them. The long but narrow and rather low islands of Choiseul and Ysabel lack many species common to Bougainville at one end and Guadalcanal at the other, while the few differentiating forms which they do possess link them rather more with the former. The low-lying Russell group has a poorly-differentiated fauna reminiscent of those of the more isolated islands, but with a surprising number of endemic subspecies. The avifauna of Malaita can be derived almost entirely from that of Guadalcanal, but has many very distinct representatives. Still more distinct, and showing some special affinities both with the Northern Islands and with Guadalcanal, the New Georgia Group is distinguished by marked internal variation, in five species and superspecies, upon which its subdivision is largely based. Though New Georgia is the largest island of the group, the taller volcanic cone of Kolombangara supports the richest avifauna.

Ornithological Literature

The avifauna of the Solomons is admirably summarized (Mayr, 1945*a*), in a work indispensable in the field or study which embodies otherwise unpublished records and taxonomic judgements. A series of papers on Northern Melanesia as a whole (Mayr, 1945*b* ; 1949*b* ; 1955 ; 1957) is unfortunately incomplete ; so that no comprehensive recent work treats the pigeons, parrots, kingfishers, or several other non-passerine groups, of the Bismarcks. The *Novitates Zoologicae* (to 1932) and the *American Museum Novitates* (from 1924) are the richest sources for revisions which include Northern Melanesian birds.

Mayr (1955) lists the most important regional works on Northern Melanesia, dating from 1899 to 1951. Several subsequent papers, some based largely on field observations, have to be added (Bradley, 1957 ; 1962 ; Bradley & Wolff, 1956 ; Cain & Galbraith, 1955 ; 1956 ; 1957 ; French, 1957). The latest development is the exploration of mountains on New Britain, which have already yielded two remarkable new species (Gilliard, 1960*a* & *b*). Mayr omits several papers based largely on field observations (Dahl, 1899 ; Donaghho, 1950 ; Hamlin, 1931 ; Meyer, 1927 ; 1930 ; 1933 ; 1937). Useful details may be gleaned from earlier works, and miscellaneous papers also omitted (Beecher, 1945 ; Danis, 1938 ; Davidson, 1929 ; 1934 ; Hartert, 1908 ; 1929 ; Mayr & Camras, 1938 ; Ogilvie-Grant, 1887 ; 1888 ; Ramsay, 1879*a* & *b* ; 1881 ; 1882*a*, *c* & *e* ; 1883 ; Schönwetter, 1935 ; Sharpe, 1888 ; Sibley, 1946 ; Stresemann,


160°E
9°30'S
Pt. Cruz
Honiara
Matanikо R.
Mt. Austen 1650
Betikama R.
Tenaru
Nalimbu R.
Tenaru R.
160
(Tsea)
Belaha R.
2500
Betilonga R.
Betilonga 1860
Mangapahu
Nunukama R.
Tasi R.
Betibau R.
Mt. Tambunugnu 5468
(? Tambunangu 6000)
Nala (1600)
(? Bitsaho 2600)
Turahi
(? Vatuvulele 5000)
(? Turipava 4100)
Mt. Popamanasiu
8005
Rivers & streams
Main watershed
Paths (approximate)
Roads
Heights in feet
0
1
2
3
4
5
6
7
8
9
10
Miles

Map 2. Localities visited on Guadalcanal (from D.C.S. 1955, sheets 2, 3, 6, 7, 10 and 11, with modifications from Grover, 1955 and 1960). Names and altitudes obtained by the expedition are shown in parentheses, and uncertain localities are indicated by queries.

1933; Tristram, 1879; 1882; 1892; 1894; 1895; White, 1938). However, the earlier locality records must be treated with reserve: Ramsay's unreliability in this respect has been repeatedly remarked. Still earlier reports are now of mainly nomenclatural importance (see Mayr (1933*b*) on Sclater's (1869) ostensible Solomons collection).

Though ecological interactions, and geographical variation in ecology and behaviour, present some of the most interesting problems in the Solomons avifauna, very little information is avilable. Field notes and locality records from the Whitney Expedition must be a rich source of unpublished data, especially on the geographical variation of altitudinal distribution (see Mayr, 1945*a* on *Rhipidura rufifrons* and *Pachycephala pectoralis*). Fairly comprehensive field-notes have been published for areas on Bougainville (Virtue, 1947), New Georgia (Sibley, 1951), Guadalcanal (Donaghho, 1950; Cain & Galbraith, 1956), San Cristoval and Ugi (Cain & Galbraith, 1956), and Rennell (Bradley & Wolff, 1957). Comparison of major islands, and of altitudinal zones, has been attempted only by Cain & Galbraith (1956).

Collecting Localities

At the time of the Oxford expedition, the best available maps of the Solomons were the American military series at 1 : 500,000 (A.M.S. X401), and larger maps of individual islands prepared by the Lands Department; both useless for inland localities. Sketch maps at 1 : 50,000 are now available for Guadalcanal (D.C.S. 1955) and for San Cristoval, Ugi, Bio, the Three Sisters, Santa Ana, Santa Catalina, and Ulawa (D.O.S. 1958). Maps 2 and 3 are based on the appropriate sheets of these, with additions from Geological Survey maps of Guadalcanal (Grover, 1955 figs. 9 & 48; 1960 fig. 42), and a sketch-map of eastern San Cristoval provided by Mr. R. B. M. Thompson.

Only localities at which collections were made are listed here. Native collectors based at these localities ranged for several miles in search of specimens. Cain & Galbraith (1956 : 106) briefly describe all the localities visited. They use a more phonetic spelling than the official form, rendering the Melanesian " b " as " mb " and the San Cristoval " g " as " gh ".

Guadalcanal: Tenaru. Tenaru Mission School on coastal plain, among grassland, lowland forest, second-growth jungle, and cultivated land.

Guadalcanal: Tsea. Waterfall on Tenaru River near sea-level (see Grover, 1955 fig. 9 & pl. VIII), in lowland forest with gardens and second growth.

Guadalcanal: Betilonga. Village near floor of Betilonga basin at 1,800 ft (see Grover, 1955 Ch. XXIV; Hill in Grover, 1960 Rept. 21). Hill forest on ridges rising to about 2,500 ft, with clearings and second growth.

Guadalcanal: Nala. Deserted village on spur above Tasi (? Baliai) River at about 1,600 ft, at foot of Kavo range (see Grover, 1960 fig. 42). Village clearing and extensive second growth in hill forest.

Guadalcanal: Turipava. Camp on spur of Kavo range above Nala, at about 4,000 ft in lower mist forest. The position of the spur was determined, from the drainage pattern of the area and compass bearings taken from about 5,000 ft at Vatuvulele, before publication of the map (Grover, 1960 fig. 42) confirmed the positions of the

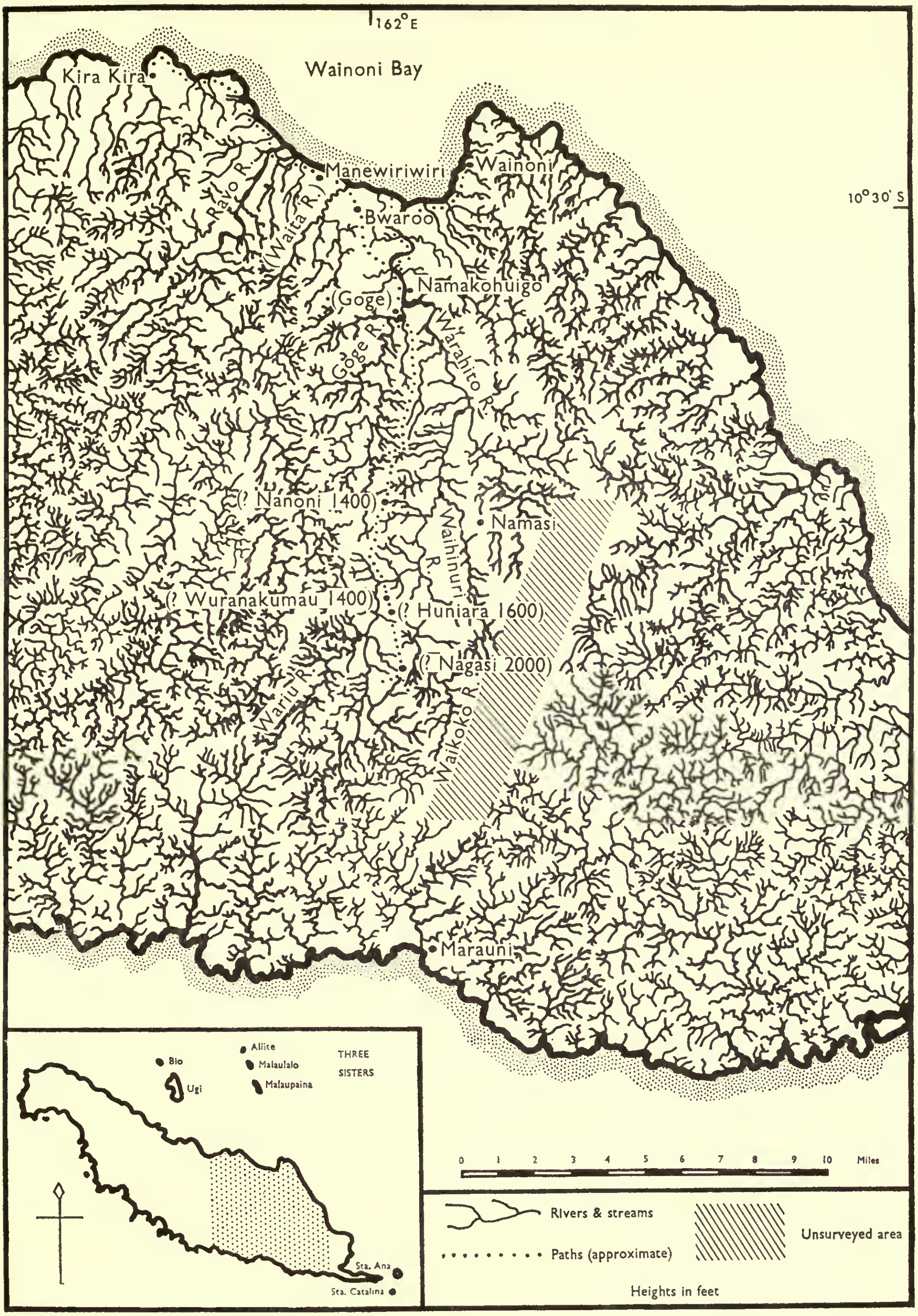
Nunukama/Betibau confluence and Nala. The peak marked as Mt. Tambunugnu at 5,300 ft may well be the high point recorded by Cain & Galbraith as Tambunangu (" forbidden to speak ") at about 6,000 ft, but the position of the sites along the spur is conjectural.

San Cristoval : Manewiriwiri. Village on coast of Wainoni Bay, among coconut plantations, gardens and second growth in coastal forest.

San Cristoval : Goge. Village in Warihito valley at Goge confluence, near sea-level in lowland forest with extensive clearings and second growth. The name of the village is correctly Napagiwae ; but this was not used by the natives during I. C. J. G.'s stay, and is ignored here for ease of reference to Cain & Galbraith (1956) and the specimen labels.

San Cristoval : Nagasi. Inland ridge rising to about 2,200 ft, with hill forest, second growth and deserted village clearing. The position of this ridge is very uncertain, and merely suggested on map 3. Unfortunately, no compass directions were recorded, and no views of recognizable points were obtained. The following may later assist in the identification of the Nagasi ridge. Crossing the Goge River from Goge, the path southwards up the crest of the nearby ridge was followed (through a deserted village, Nanoni, at about 1,400 ft after 2 hr.), without descending appreciably or crossing water until, after a sharp descent to the left from a ridge at about 1,700 ft, a small river, Halauma, flowing from right to left, was reached in 3 hours rapid marching. A recently deserted village, Wuranakumau, lay across this and 10 minutes climb away, at about 1,400 ft on a platform of the Nagasi ridge. The path to the highest point, from which the return to Wuranakumau took 40 minutes rapid descent, approximately followed the crest, past overgrown sites, Huniara at about 1,600 ft, and Nagasi at about 2,000 ft. Above Huniara it crossed a swampy saddle, with water trickling to the right. Just above Nagasi the path branched ; the left-hand branch was said to go towards the south coast, the other back to the Goge path. A view from the left of the latter showed at least three parallel ridges at about 2,000 ft, separated by steep valleys. Both paths soon began to descend. Thompson (*in litt.*), who had previously visited Namasi, made enquiries in the Wainoni area, and was convinced that the Halauma was the Haruta or upper Warihito River, where there was once a village Kehaha at the crossing (names not shown in map 3), and that the Nagasi ridge lay between this and the Waiakoko River, while the path down from the ridge probably reached the south coast at Marauni. The only discordant point is a clear though restricted view, to the right of the path below Nagasi, sharply down to a steep shore at an acute angle to the ridge, and an apparently extensive body of water. It seems impossible, from the distances involved, that this could have been the south coast as I. C. J. G. supposed at the time ; and hardly possible that it could have been the shore of a large unknown lake in the area not covered by aerial photographs (D.O.S. 1958 sheet 7).

Ugi. Although the collectors worked from the mission school at Pawa, they ranged over at least the southern half of the island, and did not collect within the extensive grounds of the school. The island reaches a height of 570 ft, and supports a variety of habitats—lowland forest, old and new second growth, gardens of native and European types, fields, coconut plantations and coastal formations.


162° E
Wainoni Bay
Kira Kira
Rayo R.
(Waita R.)
Manewiriwiri
Wainoni
10° 30' S
Bwaroo
Namakohuigo
(Goge)
Goge R.
Warahito R.
(? Nanoni 1400)
Namasi
Waihinuri R.
(? Wuranakumau 1400)
(? Huniara 1600)
(? Nagasi 2000)
Wariu R.
Waikoko R.
Marauni
Bio
Aliite
Malaulalo
Malaupaina
THREE SISTERS
Ugi
Sta. Ana
Sta. Catalina
0
1
2
3
4
5
6
7
8
9
10
Miles
Rivers & streams
Paths (approximate)
Unsurveyed area
Heights in feet

MAP 3. Localities visited on San Cristoval (from D.O.S. 1958, sheets 2, 4, 5, 7 and 8). Names and altitudes obtained by the expedition, are shown in parentheses, and uncertain localites are indicated by queries.

The distinction drawn by Cain & Galbraith (1956), between hill forest on Guadalcanal (Betilonga) and " ridge forest " at comparable altitudes on San Cristoval (Nagasi), is probably not tenable. Intensive botanical study would be necessary to establish a real difference between primary forest at about 2,000 ft on the two islands, since forest physiognomy is considerably subject to local influences, while old second growth (especially common on San Cristoval—Walker, 1948 : 49) may be misleading. Avifaunally, the evidence is at most suggestive. *Phylloscopus trivirgatus* is the only species, taken at Nagasi, which was present on Guadalcanal in the montane mist forest (Turipava) but absent from Betilonga. *Edithornis silvestris, Vitia parens* and *Rhipidura fuliginosa*, not known to be represented on Guadalcanal, might prove to be hill forest birds on San Cristoval ; as might *Zoothera margaretae* on both islands. Besides *Phylloscopus*, the only other species known from both islands, and strictly montane on Guadalcanal, is *Petroica multicolor*, whose altitudinal distribution on different islands has not been recorded (Mayr, 1934*b*)—though " above 1800 feet " (Mayr, 1945*a*) may well refer only to San Cristoval. The attempt to delimit zones of bird life in the Solomons, to study their boundaries, and to compare strictly similar habitats on different islands, has yet to be made.

THE LAND AND FRESHWATER BIRDS

Although the expedition was concerned only with the land and freshwater birds (in the sense of Mayr, 1945*a*, the Charadriformes, Procellariiformes, Phaethontidae, Sulidae and Fregatidae being neglected), a very few waders were taken incidentally :

Actitis hypoleucos (Linnaeus, 1758). Guadalcanal : Betilonga 1 unsexed 25th August ; Tenaru 1 ♀ 15th September. San Cristoval : Goge 1 ♂ 30th October, 1 ♀ 3rd December, 2 unsexed 2nd and 3rd November.

Heteroscelus incanus brevipes (Vieillot, 1816). San Cristoval : Goge 1 ♀ 27th October.

Calidris acuminata (Horsfield, 1821). San Cristoval : Goge 1 ♂ 14th November, 1 unsexed 29th October. Ugi : Pawa 1 unsexed 19th December.

The *Heteroscelus*, in winter plumage, was identified subspecifically according to Stickney (1943). As Bull (1948) found, the white bars on the upper tail-coverts are poorly developed.

Every species and subspecies of land and freshwater bird known from the islands of Guadalcanal, San Cristoval, Ugi, the Three Sisters and Santa Ana is listed below, a total of 154 forms. Those represented in the expedition collection are shown in boldface type. The number, prefixed by " M.", associated with each name is for reference to Mayr (1945*a* : 212–280) and Cain & Galbraith (1956) : there are several gaps, while conspecific races, and sometimes species of a single superspecies, bear the same number. Additional species (marked* by Cain & Galbraith) are distinguished by letters :

A. *Pelecanus conspicillatus* (p. 14)
B. *Egretta intermedia* (p. 15)
C. *Platalea regia* (p. 16)
D. *Circus approximans* (p. 19)
E. *Falco peregrinus* (p. 19)
F. *Poliolimnas cinereus* (p. 22)
G. *Cichlornis whitneyi* (p. 52)
H. *Gymnorhina tibicen* (p. 71)
J. *Myzantha melanocephala* (p. 75)

The names adopted are those used by Mayr (latest of 1941*a* ; 1945*a* ; 1945*b* ; 1949*b* ; 1955 ; 1957), except as otherwise discussed under " Notes ". Nomenclatural references are not given, since these are easily found (especially from Mathews, 1927–30 ; 1931 ; 1932 ; 1933). Reference is made to recent revisions where possible, otherwise to a standard work (usually the *Catalogue of Birds in the British Museum*, London 1874–98, cited by volume as *Cat. Birds B.M.*), or in a few cases to several partial discriminations. References to Mayr, 1945*a* are given for species not there recorded from the Solomons. More general references are introduced by " See . . .".

In the range indications, " Solomons " includes only the islands from Buka to Santa Ana, and not Nissan, Ongtong Java, Rennell, Bellona or the Santa Cruz group. Forms which are not native residents of the Solomons are indicated as introduced, migrant or straggling ; those which are not normally to be found in or near the major hill-forest habitat are indicated as coastal, lowland or montane. The available information on altitudinal and ecological distribution is summarized by Cain & Galbraith (1956).

In the sections on the specimens collected, sexes and growth-stages are indicated by: ♂, male; ♀, female; ?, unsexed; ad, adult; subad, subadult; imm, immature; juv, juvenile; nest, nestling; ret, retarded phase. A few unsexed specimens (mainly adult males of strongly dimorphic forms) have been sexed by plumage. Growth-stages were determined from plumage. Most of the specimens are in the British Museum (Natural History), referred to as BM(NH), but some are indicated as having been sent to the American Museum of Natural History (AMNH) or the Oxford University Museum (OUM). The destination of a few specimens in spirit has not yet been decided. The BM(NH) specimens are registered as nos. 1959.21.1–1590, 1604–1611.

Specimens were collected at the various stations between the following dates in 1953 (expedition serial numbers in parentheses) :

Betilonga	4th June–24th July (1–27, 31–337)
	3rd August–12th August (356–443)
	22nd August–29th August (563–613)
Tsea	9th June–10th June (28–30)
Turipava	30th July–31st July (338–348)
	15th August–20th August (444–562)
Nala	31st July–1st August (349–355)
Tenaru	3rd September–24th September (614–834)
Goge	8th October–14th November (835–1404)
	30th November–3rd December (1573–1648)
Nagasi	18th November–26th November (1405–1572)
Manewiriwiri	6th December–8th December (1649–1712)
Pawa	14th December–30th December (1713–2003)

From 26th October to 31st October (nos. 1115–1191), the native collectors were working unsupervised, recording sex and gonadial development pictorially, but not weights nor colours. These determinations seem wholly reliable : there is a reasonable proportion of undetermined specimens, and the recorded gonadial states do not conflict with the plumage, even where external differentiation is inconspicuous. Labels from this period are marked " nat. coll.". All other specimens were sexed, weighed and described by A. J. Cain or I. C. J. G.

The freshly collected birds, if not severely damaged, were weighed without allowance for loss of blood and feathers or for lodged shot. Weights less than 185 gm were taken to the nearest 0·5 gm, with a long-scale spring balance designed by Dr. J. A. Gibb for weighing small passerines alive (as advertised by the B.T.O. in *Bird Study*). Used with a 50 gm weight for the lighter specimens, this gave a linear response over its whole range, and would have been reliable to a greater degree of accuracy. It was calibrated in the field, and checked at intervals. Weights between 185 and 500 gm were taken with a dietary balance to the nearest 5·0 gm, and their means are given to the nearest 1·0 gm. Weights of discarded and spirit specimens have been used where possible, so that a weight series may be longer than the corresponding series of skins. Linear measurements were almost all taken by E. H. G., while remeasurement of some series by I. C. J. G. showed good agreement. Except where otherwise stated, wings were measured flattened down, tails from the common sheath to the tip of the longer central rectrix, and bills from the angle of skull and culmen chordwise to the tip of the mandible.

Weights are given in grams, linear measurements in millimetres, to the nearest 0·5 unit, and their means to the nearest 0·1 unit (except for weights above 185 gm). Measurements of unsexed specimens are not usually given. Though the standard deviation should ideally be given as the measure of spread, the undesirability of combining or accurately comparing measurements made by different workers makes the labour of computation not worthwhile in reports on collections, and the range is here given instead. Three or more measurements are given in the form : *number of individuals measured/sex/stage/range/(mean)* ; e.g. 5 ♂ ad 42·5–52 (46·7). For 2 specimens, the measurements are given instead of the range and mean.

Descriptions of the colours of soft parts are compiled from the field-labels for each series, including those of discarded and spirit specimens. They apply to both sexes and all represented stages, unless otherwise stated ; stages represented but not mentioned agree with the next older stage. Other notes on individual specimens refer to those taken by the expedition, unless otherwise noted. In the colour-comparison of *Ptilinopus solomonensis* and *Aplonis metallica* (pp. 24 and 68), the longest and most variable series was divided into as many colour-classes as could be re-assembled with little error, to which the remaining series were then matched, rather than into a predetermined number of classes.

(A) *Pelecanus conspicillatus* Temminck, 1824

REFERENCES. *Cat. Birds B.M.* 26 : 483 ; Alexander, 1954 : 189.

RANGE. Australia ; straggling from Tenimber Isles to Melanesia (coasts and lowlands).

NOTES. Recorded from the Solomons, New Hebrides and Rennell after high winds in 1952 (Anon, 1952 ; Dorst, 1954 ; Laird, 1954 ; Bradley & Wolff, 1956 ; Cain & Galbraith, 1956).

(M. 2) ***Phalacrocorax melanoleucos melanoleucos*** (Vieillot, 1817)

References. Amadon, 1942*a* : 2.

Range. Java and Celebes to Australia and Santa Cruz, including Guadalcanal and Santa Ana (lowlands).

Specimens. Guadalcanal : Betilonga 1 ♀ ad. To OUM.

Bill 42.

Iris dark brown, silvery outer ring. *Skin* round eye yellowish fuscous, chin dirty yellow. *Bill* yellow, maxilla mottled with black. *Foot* black.

Notes. The known range of this species is irregular. In the Solomons proper, it is well-known from Guadalcanal (Mayr, 1945*a* ; Donaghho, 1950 ; Cain & Galbraith, 1956) and Santa Ana (Mayr, 1945*a* ; French, *in litt.*), while the endemic race *brevicauda* occurs on Rennell. A single specimen has been recorded from Bougainville (White, 1938), though the species is not known from the Bismarcks. Another, hitherto unrecorded, was taken at Star Harbour, San Cristoval, by Commander J. F. A. O'Neill of the Melanesian Mission's m.v. " Southern Cross ". It was examined by I. C. J. G. at Pawa in January 1954, but was later lost when the refrigerator broke down (Turbott, *in litt.*).

Though liable to be neglected by collectors, the species is conspicuous where it occurs. Virtue (1947) on Bougainville and Sibley (1951) on New Georgia apparently did not study suitable habitats on lakes or large rivers, so that their failure to record it is not conclusive. However, it definitely does not seem to maintain itself on San Cristoval. French (*in litt.*) doubts its presence there, natives did not recognize its unmistakable description, and it was not seen during six weeks on the apparently suitable Warihito River. The Star Harbour specimen must surely have been a straggler from Santa Ana, across the three-and-a-half mile strait.

The presence of the species on several small or low-lying islands without rivers (e.g. Santa Ana, Rennell, Ticopia) clearly depends on their possession of freshwater lagoons. However, its absence from such large islands as San Cristoval is surprising.

(M. 3) ***Butorides striatus solomonensis*** Mayr, 1940

References. Mayr, 1940*a* : 6. See Bock, 1956.

Range. Solomons (lowlands).

Specimens. Guadalcanal : Bilaha, Tenaru R. 1 ♂ ad.

Weight 245. *Wing* 181. *Tail* 64. *Bill* (from feathering) 66·5.

Iris bright yellow. *Eyelid* dull cherry-red. *Skin* round eye pale brown. *Bill* maxilla black, mandible dirty white. *Foot* dirty fuscous green, shank bright yellow behind, sole dirty yellow.

Notes. We follow the generic arrangement of Bock (1956) for the Ardeidae.

(B) *Egretta intermedia plumifera* (Gould, 1848)

References. Amadon & Woolfenden, 1952 : 11. See Bock, 1956.

Range. Australia, New Guinea region, southern Moluccas (lowlands) ; San Cristoval—straggler ?

Notes. The young bird taken by French at Kira Kira (Cain & Galbraith, 1956; French, 1957) may have been a straggler. However, the extensive marshes of San Cristoval (Grover, 1958) provide a habitat suitable for the species, which because of its wariness and inaccessibility was not for a long while recognized as widespread and locally common in New Guinea (Rand, 1938 : 291).

(M. 4) *Egretta sacra sacra* (Gmelin, 1789)

References. Mayr & Amadon, 1941 : 3. See Bock, 1956.

Range. Asia to western Polynesia (coasts and lowlands).

(M. 5) **Nycticorax caledonicus mandibularis** Ogilvie-Grant, 1888

References. Amadon, 1942*a* : 5. See Bock, 1956.

Range. Solomons, Nissan and New Ireland—intergrading via Bismarcks with *N.c. hilli* (lowlands).

Specimens. Guadalcanal: Betilonga 2 ♂ ad, 1 ♀ ad. 1 ♂ ad to OUM.

Wing 2 ♂ ad 270, 272; 1 ♀ ad 262. *Tail* 1 ♂ ad 95. *Bill* (from feathering) 2 ♂ ad 66·5, 69·5; 1 ♀ ad 63·5.

Iris yellow. *Skin* round eye dull yellow or yellow-green. *Bill* black, ♀ mandible yellowish. *Foot* yellow.

(M. 6) *Ixobrychus flavicollis woodfordi* (Ogilvie-Grant, 1888)

References. Mayr, 1945*b* : 5; Bradley, 1962 : 11. See Bock, 1956.

Range. Solomons and Rennell (lowlands).

Notes. This apparently widespread, though rare or retiring, species has not yet been recorded from the San Cristoval group In addition to the localities already recorded (Mayr, 1945*a*), there is a specimen in the BM(NH) collected at Bouin, Bongainville by W. F. H. Rosenberg.

(C) *Platalea regia* Gould, 1838

References. Mayr, 1945*a* : 280; Amadon & Woolfenden, 1952 : 5.

Range. Australia, straggling as far as Celebes, Rennell and New Zealand (lowlands).

Notes. We follow Amadon & Woolfenden in regarding *regia* as a distinct species. It is recorded as a rare non-breeding visitor to the Three Sisters (French, 1957), perhaps from Rennell where it may be resident (Bradley & Wolff, 1956 : 92).

(M. 7) **Anas poecilorhyncha pelewensis** Hartlaub & Finsch, 1872

References. Amadon, 1943*a* : 3.

Range. Micronesia and northern New Guinea to Polynesia (lowlands).

Specimens. Guadalcanal: Betilonga 1 ♀ ad. To OUM.

Wing 217. *Bill* (from feathering) 46·5.

Iris light brown. *Bill* bluish grey. *Foot* dull fawn.

Notes. We follow Delacour & Mayr (1945 : 21) in uniting specifically the *superciliosa* group of Australasian mallards with *luzonica* of the Philippines and *poecilorhyncha* of

Malaysia and southeast Asia. The species has been recorded from the San Cristoval Group only by Ramsay (1882*c* : 41), but was familiar to natives of Goge (Cain & Galbraith, 1956 : 117).

(M. 8) ***Aviceda subcristata gurneyi*** (Ramsay, 1881)

REFERENCES. Mayr, 1945*b* : 9.

RANGE. Guadalcanal, Malaita and San Cristoval Group (mainly lowlands).

SPECIMENS. Guadalcanal : Betilonga 1 ♀ ad. To OUM.

Weight 340. *Wing* 316. *Tail* 193. *Bill* 30.

Iris bright yellow. *Bill* maxilla black, cere and mandible pale silvery blue. *Foot* white.

(M. 9) ***Haliastur indus flavirostris*** Condon & Amadon, 1954

REFERENCES. Condon & Amadon, 1954 : 206.

RANGE. Feni, Duke of York, Solomons (mainly coasts and lowlands).

SPECIMENS. Ugi 1 ? juv.

Wing 375. *Bill* 136·5.

Iris dark brown. *Eyelid* dark slate, visor and skin round eye dirty yellowish-green. *Bill* blackish slate streaked with bluish grey, gape dull greenish yellow, cere slaty black. *Foot* lemon-yellow, claws black.

The bills of this specimen and two BM(NH) juveniles are conspicuously heavier than those of *girrenera*, though not paler in the skin.

NOTES. A BM(NH) subadult specimen from the Duke of York group has the heavy and wholly yellow bill characteristic of this race ; which—with *Ptilinopus viridis lewisi*, *Ducula pistrinaria pistrinaria*, *Eos cardinalis*, *Hemiprocne mystacea woodfordiana*, *Eurystomus orientalis solomonensis* and *Hirundo tahitica subfusca* (and probably *Tyto alba* cf. *crassirostris*)—is a form characteristic of the Solomons which has colonized certain small islands in the Bismarcks.

(M. 10) *Accipiter meyerianus* (Sharpe, 1878)

REFERENCES. Mayr, 1934*a* : 1.

RANGE. Moluccas, Japen, Bismarcks, Solomons—Kolombangara, Guadalcanal (mountains ?).

NOTES. This very rare species is known in the Solomons by two specimens (Hartert, 1929 : 5).

(M. 11) ***Accipiter novaehollandiae pulchellus*** (Ramsay, 1882)

REFERENCES. Hartert, 1929 : 4. See Mayr, 1945*b*.

RANGE. Guadalcanal (mainly lowlands).

SPECIMENS. Guadalcanal : Tenaru 1 ♀ ad. To OUM.

Weight 280. *Wing* 221. *Tail* 173. *Bill* 29.

Iris very dark reddish brown. *Eyelid* dull orange, visor dull yellow. *Bill* black, cere and base orange. *Foot* orange, claws black.

This specimen (OUM No. B/3978) is uncharacteristic, and differs from three

BM(NH) females of *pulchellus* from Tenaru and Lunga, in having much deeper rufous thighs and under tail-coverts, not contrasting strongly with the belly, and somewhat more rufous on the under wing-coverts. However it agrees with *pulchellus*, and differs from *rufoschistaceus-rubianae-bougainvillei*, in having the thighs and under tail-coverts decidedly paler than the belly, the under wing-coverts primarily grey-and-white-speckled rather than solid rufous, and extensive white areas at the bases of the inner webs of the wing quills.

(M. 12) ***Accipiter albogularis woodfordi*** (Sharpe, 1888)

References. Mayr, 1957 : 7.

Range. Main Chain of the Solomons, Bougainville to Ulawa.

Specimens. Guadalcanal : Betilonga 1 ♂ ad, 1 ♀ ad, 1 ♀ imm. 1 ♂ ad to OUM.

Weight 1 ♂ ad 265 ; 1 ♀ imm 335. *Wing* 1 ♂ ad 210 ; 1 ♀ ad 248 ; 1 ♀ imm 241. *Tail* 1 ♂ ad 146 ; 1 ♀ ad 123. *Bill* 1 ♂ ad 26 ; 1 ♀ ad 30 ; 1 ♀ imm 28·5.

Iris orange ; imm yellow. *Eyelid* yellow, visor fuscous green, skin of chin greenish yellow. *Bill* ♂ black, base of mandible pale blue-grey ; ♀ dark grey, base of mandible white ; cere greenish yellow ; imm bill fuscous-streaked. *Foot* yellow, claws black.

The immature resembles a juvenile in the normal (i.e. not the " *holomelas* ") phase, but has the mantle blacker, the ground-colour of the underparts almost pure white, the underwing with bold chevrons rather than narrow shaft-streaks, and the thighs with pale rufous chevrons and a few sub-basal bars rather than shaft-streaks. The adults are both in the normal phase, with the rufous collar slightly developed.

(M. 12) ***Accipiter albogularis albogularis*** Gray, 1870

References. Mayr, 1957 : 10.

Range. San Cristoval Group.

Specimens. San Cristoval : Goge 1 ♀ ad.

Weight 280. *Wing* 243. *Tail* 170. *Bill* 29·5.

Iris deep orange-yellow. *Eyelid* deep yellow, visor pale fuscous green. *Bill* dark grey above, base and mandible pale and bluish, cere dull pale yellow-green. *Foot* orange-yellow, shanks paler and greener.

Like all specimens known from San Cristoval or Santa Ana, this is in the normal phase, without any trace of a rufous collar and with black speckling on the sides of the breast.

Notes. Two of the seven specimens in the BM(NH) are from San Cristoval : an unsexed adult and a male juvenile, both in the normal phase. The other five are among those recorded by Ramsay (1882*c* : 30) as having been collected on Ugi by Stephens. Formerly in the Gurney collection (Gurney, 1884 : 33–34, footnote 4), these have been added to the BM(NH) collection since Mayr's (1957) paper. Two are adults in the normal phase, agreeing well with specimens from San Cristoval. The remaining adult and two juveniles are in the " *holomelas* " phase, otherwise unknown outside the range of *woodfordi*. It is unfortunate that Ramsay's known unreliability over locality records makes it impossible to accept Ugi as their provenance without confirmatory evidence. Doubt of the record is increased by the fact that the locality

" Ugi Island " has been added subsequently to the labels, though in the same hand. Adults of *albogularis* cannot certainly be distinguished from *woodfordi*. However, the " *holomelas* " juveniles agree closely with each other, and differ from one such of *woodfordi*, in having the spotting of the breast give way to the barring of the belly much more gradually (in which they agree with a normal juvenile of *albogularis*, though in the latter the transition takes place much lower on the breast), the underwing with less black, and the thighs with very vague chevrons rather than shaft-streaks. It would be interesting to find the all-black "*holomelas* " phase on Ugi but not on San Cristoval, in view of the tendency towards melanism of flycatchers on the former island (*Rhipidura rufifrons ugiensis*, *Monarcha castaneiventris ugiensis*, *M. vidua squamulatus*).

(M. 14) *Haliaeetus sanfordi* Mayr, 1935

References. Mayr, 1936 : 1.

Range. Solomons.

Notes. Definitely known only from the larger islands (including Bougainville—Beecher, 1945 : 35) and the Three Sisters (Cain & Galbraith, 1956 : 106), though reported from Ulawa and Ugi (*op. cit.* : 118). Condon & Amadon (1954 : 230) discuss the status of the representative species *H. leucogaster* on Nissan.

(D) *Circus approximans gouldi* Bonaparte, 1850

References. Amadon, 1941 : 371 ; Mayr, 1945*a* : 54.

Range. Australia, southern New Guinea, Solomons, Southern Melanesia, western Polynesia, New Zealand (lowlands).

Notes. In the Solomons, known from the lowlands of Guadalcanal (Beecher, 1945 : 35) and as a rare non-breeding visitor to the Three Sisters (French, 1957).

(M. 15) *Pandion haliaetus melvillensis* Mathews, 1912

References. Amadon, 1941 : 376.

Range. Malaysia to Micronesia, Solomons and New Caledonia (coasts).

(M. 16) *Falco severus papuanus* Meyer & Wigglesworth, 1893

References. Mayr, 1945*b* : 11.

Range. Celebes to New Guinea and Northern Melanesia.

Notes. In the Solomons, known from Bougainville (Sibley, 1946 : 97) and Gizo (Mayr, 1945*b*), and doubtfully recorded from Guadalcanal (Cain & Galbraith, 1956 : 119).

(E) *Falco peregrinus ernesti* Sharpe, 1894

References. Mayr, 1941*c* : 1 ; 1945*a* : 56.

Range. Malaysia to Philippines, New Guinea region and Northern Melanesia.

Notes. In the Solomons, known only as a rare non-breeding visitor to the Three Sisters (French, 1957 ; see Cain & Galbraith, 1957).

(M. 17) ***Megapodius freycinet eremita*** Hartlaub, 1867

References. Mayr, 1938*a* : 12.

Range. Northern Melanesia, with irregular minor geographical variation (coasts and lowlands).

Specimens. Guadalcanal : Betilonga 1 ♂ ad, 2 ♀ ad. San Cristoval : Goge 1 ♂ ad, 1 ? juv. 1 ♀ ad to OUM.

Weight 1 ? juv 68. *Wing* 2 ♂ ad 221, 227 ; 2 ♀ ad 225, 227 ; 1 ? juv 55. *Tail* 1 ♂ ad 72 ; 2 ♀ ad 71, 73. *Bill* 2 ♂ ad 28, 29·5 ; 2 ♀ ad 26·5, 27 ; 1 ? juv 14.

Iris brown ; juv grey-brown. *Skin* of throat and sides of face dull purplish-red to dull pink, crown strawberry ; juv throat pinkish-brown. *Bill* yellow, greenish basally ; juv dark fuscous grey. *Foot* dark olive green to blackish fuscous ; juv dark grey-brown.

Notes. Frith (1956) summarizes the incubation methods of megapodes, which seem to be especially diverse in the Solomons.

(M. 18) ***Turnix maculosa salomonis*** Mayr, 1938

References. Mayr, 1938*b* : 3 ; Sutter, 1955 : 114.

Range. Guadalcanal (lowlands).

Specimens. Guadalcanal : Tenaru 3 ♂ ad, 1 ♂ juv, 1 ♀ ad. 1 ♂ ad to AMNH.

Weight 3 ♂ ad 38·5, 39·5, 41 ; 1 ♂ juv 31 ; 2 ♀ ad 52·5, 57·5. *Wing* 3 ♂ ad 75, 76, 77 ; 1 ♂ juv 72 ; 1 ♀ ad 86. *Tail* 3 ♂ ad 27, 27, 28 ; 1 ♂ juv 23·5 ; 1 ♀ ad 31·5. *Tarsus* 3 ♂ ad 19·1, 19·5, 20·3 ; 1 ♂ juv 19·4 ; 1 ♀ ad 22·4. *Culmen* (dorsal) 3 ♂ ad 9·5, 10·0, 10·7 ; 1 ♂ juv 10·7 ; 1 ♀ ad 11·5 ; (lateral) 3 ♂ ad 11·1, 11·7, 11·7 ; 1 ♂ juv 11·0 ; 1 ♀ ad 12·8. Linear measurements taken by Sutter.

Iris yellowish white. *Bill* blackish, base of mandible yellowish, gape bright yellow ; whole of juv mandible and edge of maxilla dull yellow. *Foot* dull yellow, toes greyer.

Four other specimens of this race have been recorded : an adult female at the AMNH (Mayr, 1938*b*), an adult female at the Museum of Vertebrate Zoology, Berkeley, California, and an adult male at the Chicago Museum (Beecher, 1945), and a juvenile female at the U.S. National Museum (Baker, 1948 ; Sutter, 1955). Dr. Sutter has kindly examined our specimens and provided very helpful notes, though comparative material of the other eastern races was not available to him at the time. All the specimens have the black markings well-developed on the underparts, but none approaches the remarkable condition shown by the juvenile in the USNM (Sutter, *in. litt.*).

The female specimen is in poor condition on rump, back and throat, and adds little to Mayr's description ; except that the belly is decidedly paler and the back apparently less grey than those of *saturata*. It differs from five adult females from the central highlands of New Guinea (in the type-series of *giluwensis* Sims, 1954) in having the plain rufous feathers of the mid-breast darker, contrasting more with the paler black-barred feathers at the sides ; the belly darker than average, matching the most rufous-tinged belly of *giluwensis* ; the head paler, with wider grey edges, and without a distinct pale stripe ; the rufous collar well-developed (only one *giluwensis* has concentrations of rufous near the wing-roots) ; and the upper back more rufous. It differs from three adult females from New Britain (including the holotype of *saturata*) in having the belly and perhaps the throat paler ; the black-barred feathers of the breast perhaps encroaching more towards the mid-line ; the rufous collar much better-developed than in the one *saturata* which shows it (see Mayr, 1938*b*) ; and the back apparently with more rufous and *more* black. The head is similar to those of two *saturata* which lack crown-stripes. This specimen differs from a female from south-eastern New Guinea (holotype of *horsbrughi*) in having the belly much paler (the holotype being unusual among *horsbrughi* in having the belly rufous—see Mayr, 1938*b* : 2 ; Sutter, 1955 : 111) and the throat possibly so ; more barring on the breast, with the barred feathers more conspicuously pale ; the edges of the upper wing-coverts much paler ; and the crown with broader grey edges and no central stripe. It differs from two adult females from Cape York Peninsular (*yorki*) in having the midbreast deeper rufous ; more barring on the sides of the breast ; the crown-stripe less distinct ; the collar deeper rufous and apparently narrower ; and the mantle apparently blacker, less grey.

The male has not hitherto been described. Sutter (*in litt.*) describes the three adults as " in coloration and pattern somewhat intermediate between *horsbrughi* and *mayri* of the Louisiades. Upper-parts in general appearance rather plain-coloured (apart from the ochraceous edges on mantle and scapulars), principal colours black and dark olive-grey with narrow rufous vermiculation or bars. The rufous bars are distributed regularly over the whole upper back, without indication of a nuchal collar (as in Australian males). Breast rather deep rufous, middle of belly whitish in strong contrast to the breast collar colour (as in *giluwensis*). Sides of the breast and wing-coverts heavily spotted." These specimens agree with two males of *giluwensis* in the coloration of the underparts and in the crown-stripe, and differ in having the pale edges of the crown-feathers wider and more rufous ; the back variable but averaging greyer, less black, and more rufous towards the interscapulars ; and the edges of the scapulars and upper wing-coverts deeper ochraceous. They differ from three adult males of *saturata* in having the belly-patch whiter and larger ; the edges of the crown-feathers more rufous, less grey ; the mantle more black, less grey, with considerably more rufous anteriorly ; and the edges of the upper wing-coverts and scapulars deeper ochraceous.

NOTES. Mayr (1949*b* : 2) combines *T. maculosa* specifically with *T. sylvatica*, but they overlap on Mindanao (Sutter, 1955 : 137). Pendleton (1947) studied this race in the field.

(M. 19) ***Rallus philippensis christophori*** Mayr, 1938

REFERENCES. Mayr, 1938*b* : 7.

RANGE. Guadalcanal and San Cristoval Groups.

SPECIMENS. San Cristoval : Goge 1 ♀ ad.

Weight 240. *Wing* 134. *Bill* 34.

Iris reddish-brown. *Bill* slate, mandible paler, base pinkish-brown. *Foot* pale greyish-buff, joints greyer.

The specimen, caught in a native drop-trap, is in poor condition posteriorly.

(F) *Poliolimnas cinereus leucophrys* (Gould, 1847)

References. Mayr, 1949*b* : 17.

Range. Moluccas to northern Australia and Northern Melanesia (lowlands).

Notes. Known in the Solomons from Bougainville (Baker, 1948) and Guadalcanal (Donaghho, 1950) ; and from the Three Sisters (Cain & Galbraith, 1956 ; French, 1957) where it is common. No doubt, as French suggests, it will prove to be widespread.

(M. 20) *Amaurornis olivaceus ultimus* Mayr, 1949

References. Mayr, 1949*b* : 21.

Range. San Cristoval, Santa Ana, Gower (lowlands).

(M. 21) *Nesoclopeus woodfordi woodfordi* (Ogilvie-Grant, 1889)

References. Mayr, 1949*b* : 15.

Range. Guadalcanal.

(M. 22) *Edithornis silvestris* Mayr, 1933

References. Mayr, 1933*a* : 1.

Range. San Cristoval (mountains).

Notes. The species is well-known to the natives, and apparently not rare below Nagasi, yet the holotype remains unique.

(M. 23) ***Porphyrio porphyrio samoensis*** Peale, 1848

References. Mayr, 1949*b* : 22.

Range. Northern and Southern Melanesia and western Polynesia (individual and irregular geographical variation).

Specimens. Guadalcanal : Betilonga 2 ♀ ad. San Cristoval : Goge 1 ♀ ad. 1 ♀ ad to OUM.

Weight San Cristoval 1 ♀ ad 495. *Wing* Guadalcanal 2 ♀ ad 222, 226 ; San Cristoval 1 ♀ ad 203. *Tail* Guadalcanal 1 ♀ ad 86. *Bill* (from back of shield) Guadalcanal 2 ♀ ad 61·5, 64 ; San Cristoval 1 ♀ ad 57·5.

Iris orange-brown to red. *Bill* and shield deep orange-red. *Foot* flesh colour to deep pink.

The San Cristoval specimen agrees with Mayr's in being small and black above, but has a distinct breast-shield.

(M. 24) ***Ptilinopus superbus superbus*** (Temminck, 1810)

References. Stresemann, 1914 : 45 ; 1923 : 72. See Cain, 1954*b* ; 1954*c* ; 1957.

Range. Moluccas to eastern Australia and Solomons, except San Cristoval Group (mainly lowlands).

Specimens. Guadalcanal : Betilonga 3 ♂ ad, 4 ♀ ad. 1 ♂ ad, 2 ♀ ad to OUM.

Weight 4 ♂ ad 111·5–133·5 (120·4) ; 5 ♀ ad 104–118 (113·4). *Wing* 3 ♂ ad 124–129 (127·3) ; 4 ♀ ad 115–127 (121·5). *Bill* 3 ♂ ad 18·5–19 (18·8) ; 3 ♀ ad 18–19 (18·7).

Iris yellow, sometimes greenish. *Eyelid* pale yellow or green, skin round eye greenish blue. *Bill* sage green to fuscous green. *Foot* dull purplish red (" bright " in 1 of 12).

A male (not preserved) was taken by collectors from Turipava, probably below the mist-forest.

Notes. It has only recently been pointed out (Cain & Galbraith, 1956 : 121) that this widely-distributed species is apparently absent from the San Cristoval group. There are no specimens from there in the AMNH (Amadon, *in litt.*) nor the BM(NH). and natives of San Cristoval and of Ugi failed to recognize a coloured figure of this distinctive lowland species (Mayr, 1945*a* pl. 2, fig. 11). Ramsay's (1882*c* : 39) record for Ugi cannot be accepted without further evidence.

(M. 25) **Ptilinopus solomonensis ocularis** Mayr, 1931

References. Mayr, 1931*f* : 6. See Cain, 1954*b*.

Range. Guadalcanal.

Specimens. Guadalcanal : Betilonga 2 ♂ ad, 1 ♂ juv ; Turipava 2 ♂ ad, 4 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 5 ♂ ad 112–136 (125·3) ; 1 ♂ juv 91 ; 5 ♀ ad 114·5–141·5 (127·1). *Wing* 4 ♂ ad 127·5–131 (129·9) ; 1 ♂ juv 122·5 ; 3 ♀ ad 123·5–129 (125·8). *Bill* 2 ♂ ad 19, 20 ; 1 ♂ juv 20 ; 4 ♀ ad 19·5–21 (20·2).

Iris sage green (light sage green to dull green) ; juv pale yellow. *Skin* round eye pale green to bluish. *Bill* sage green to greenish-grey. *Foot* dull purplish red (" dull pink " in 1) ; juv dull reddish brown and grey.

Notes. Iris colours were not given for the three high-altitude races in the Solomons (*bistictus*, *ocularis* and *ambiguus*) at their original description (Mayr, 1931). Labels of the AMNH series of *ocularis* show some variation in iris colour (P. Vaurie, *in litt.*), but it is not clear whether the iris is ever yellow. We have the labels of ten adults, all showing it as some shade of dull green. This is very different from the warm yellow, with a narrow green inner ring, of *solomonensis*. BM(NH) specimens of lowland races have the irides indicated as bright yellow to red (*solomonensis*), yellow (*neumanni*), pale greenish yellow to dull cream yellow (*meyeri*) and pale greenish yellow (*johannis*). Careful study of the AMNH collections will be necessary to determine the geographical variation of iris colour in this species

(M. 25) **Ptilinopus solomonensis solomonensis** Gray, 1870

References. Mayr, 1931*f* : 6. See Cain, 1954*b*.

Range. San Cristoval Group.

Specimens. San Cristoval : Goge 39 ♂ ad, 27 ♀ ad, 1 ? juv ; Nagasi 5 ♂ ad, 1 ♀ ad, 1 ? juv. Ugi 1 ♂ ad, 1 ♀ ad, 1 ? juv. 3 ♂ ad, 3 ♀ ad to AMNH ; 3 ♂ ad, 2 ♀ ad to OUM.

Weight Goge 30 ♂ ad 80–101·5 (93·1) ; 22 ♀ ad 83·5–105 (93·7) ; Nagasi 6 ♂ ad 88·5–106·5 (98·1) ; 1 ♀ ad 97·5 ; Ugi 1 ♂ ad 101 ; 1 ♀ ad 86·5. *Wing* Goge 39 ♂ ad 114–123 (119·5) ; 27 ♀ ad 111·5–123 (116·8) ; Nagasi 5 ♂ ad 116–124 (120·3) ; 1 ♀ ad 120 ; Ugi 1 ♂ ad 127 ; 1 ♀ ad 119. *Bill* 40 ♂ ad 18–21 (19·3) ; 28 ♀ ad 16·5–20 (19·1).

Iris orange-yellow (pale pinkish yellow to dull orange), inner ring pale green ; juv dark grey-brown to dirty yellow, inner ring greenish. *Skin* round eye pale green to pale blue ; juv blackish to blue-green, eyelid paler. *Bill* sage-green, sometimes greyer and bluer ; juv dark, fuscous-green to blue-grey. *Foot* dull mauve, shanks redder ; juv pale pinkish brown to pale grey.

In this, and the other long series of *Ptilinopus*, the distribution of weights is markedly bimodal. However, this is not paralleled in other measurements or characters, and no first-year or retarded plumages (as described by Mayr, 1931*f* : 7, for *ambiguus*) can be discerned. The juvenile from Nagasi, presumably a male, has pink forehead feathers which evidently belong to the juvenile plumage.

The series from Goge is extremely variable in depth of coloration. This is evidently due to variation in carotenoid pigmentation (see Völker, 1953 ; Auber, 1957), the yellow, green and lilac areas being equally affected. The variation does not seem to be due to bleaching, whether in life or *post mortem*. It is most conspicuous in the green of the back, but there interacts with variation in structural coloration (blue and bronzing). Table I shows the distribution of specimens among seven colour-classes (A palest to G deepest) for the males, judged from the yellow bib ; and among 6 classes (H to N) for the females, judged from the yellow under tail-coverts. BM(NH) specimens of *solomonensis* are included in the series for the coast of San Cristoval and Ugi. Other specimens, of the races *neumanni*, *meyeri*, and *johannis*, are lumped together, since they are too few to indicate significant differences among themselves in variability or average depth of pigmentation.

TABLE I.—*Intensity of yellow carotenoid pigment in adults of* Ptilinopus solomonensis.

Classes A–G males, judged on bibs ; classes H–N females, judged on under tail-coverts : classes A and H palest, G and N deepest.

	A	B	C	D	E	F	G	H	J	K	L	M	N
P.s. solomonensis:													
Nagasi . .						1	4					1	
Goge . . .	1	4	3	3	14	5	6	1	2	3	13	7	1
San Cristoval coast.					1	1						1	
Ugi . . .					2	1					1		
P. s. ocularis . .						3	1				1		1
Other races . .					3	4	2			1	2	2	

NOTES. The subspecific assignment of the population on the Three Sisters must be tentative, since it is represented in the BM(NH) by a single juvenile only.

(M. 25) **Ptilinopus solomonensis** cf. **solomonensis**

SPECIMENS. Guadalcanal : Betilonga 1 ♂ ad.

Weight 97·5. *Wing* 121. *Bill* 19·5.

Iris yellowish orange. *Skin* round eye pale blue-green. *Bill* greyish green. *Foot* dull lilac, shanks dull purplish red.

This specimen agrees with the lowland races, and disagrees with *ocularis*, in its smaller dimensions, yellow iris, and complete lilac cap. It is richly-pigmented (group F of Table I), and has the scapular spots slightly larger and the cap and belly perhaps slightly richer lilac than in most males of *solomonensis*. It could belong to *vulcanorum* of the New Georgia Group (P. Vaurie, *in litt.*).

NOTES. Although Amadon does not rule out the possibility of this being a mutant of *ocularis* (P. Vaurie, *in litt.*), the concordance of three characters makes it much more probable that it is a straggler from another island. Its provenance must remain uncertain until the *solomonensis*-like populations on small islands in the Solomons are better known (see Mayr, 1931*f* : 8). Geographically, Buena Vista near the Florida group seems the most probable source.

Errant individuals are almost unknown among the strongly-localized races of Northern Melanesia. Their occasional occurrence is necessary to the hypothesis that character-progressions in insular areas may be due to gene-flow (e.g. Galbraith, 1956: 160–165), but they must remain rare if the geographical variation is not to be swamped. The possibility should not be overlooked, that striking character-differences between neighbouring insular populations may sometimes be of selective importance in reducing introgression from such errant individuals. This would help to explain why very isolated populations tend to lose their distinctive patterns while relatives in archipelagos, not sympatric with closely-related species, retain them.

(M. 26) ***Ptilinopus viridis lewisi*** Ramsay, 1882

REFERENCES. *Cat. Birds B.M.* 21 : 153. See Cain, 1954*b*.

RANGE. Lihir, Solomons except San Cristoval Group.

SPECIMENS. Guadalcanal : Betilonga 1 ♂ ad. To OUM.

Weight 112. *Wing* 116. *Bill* 17·5.

Iris yellow. *Bill* yellow. *Foot* dull purplish red.

(M. 26) ***Ptilinopus viridis eugeniae*** (Gould, 1857)

REFERENCES. *Cat. Birds B.M.* 21 : 153. See Cain, 1954*b*.

RANGE. San Cristoval, Ugi, Three Sisters.

SPECIMENS. San Cristoval : Goge 10 ♂ ad, 1 ♂ juv, 11 ♀ ad ; Nagasi 1 ♂ ad. Ugi 2 ♂ ad, 2 ♀ ad, 1 ♀ juv. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 13 ♂ ad 93·5–129·5 (113·8) ; 1 ♂ juv 66 ; 12 ♀ ad 101·5–127·5 (113·2) ; 1 ♀ juv 89. *Wing* 12 ♂ ad 114–128 (122·6) ; 1 ♂ juv 113·5 ; 12 ♀ ad 116–124·5 (120·2) ; 1 ♀ juv 115·5. *Bill* 13 ♂ ad 17–19 (18·2) ; 1 ♂ juv 18 ; 12 ♀ ad 17–18·5 (18·1) ; 1 ♀ juv 17·5.

Iris tawny orange to tawny red (" deep scarlet " in 2 of 3 from Ugi), inner ring (when noted) pale yellow to dull green ; juv dull brownish, inner ring greenish. *Skin* round eye bluish grey, eyelid usually yellower. *Bill* yellowish, usually greenish (sometimes golden), base and cere dull maroon ; juv dirty yellowish-green, yellower distally, cere once dull maroon. *Foot* mulberry-red, sometimes bluer ; juv dull (buffy pink to greyish purple).

The maroon-based bill of *eugeniae* has been overlooked as a further character of this very distinct race. In the dried skin the maroon turns blackish. Apart from *eugeniae*, only *geelvinkianus* shows slight blackish traces in the dried bill. Of BM(NH) specimens, only one of *vicinus* and six of nominate *viridis* have the colour in life indicated. In these the base is indicated as redder (scarlet to orange) than the tip (rich orange to greenish-yellow).

(M. 27) **Ptilinopus richardsi richardsi** (Ramsay, 1882)

REFERENCES. Ripley & Birckhead, 1942 : 8. See Cain, 1954*b* ; 1957.

RANGE. Ugi, Three Sisters, Santa Ana.

SPECIMENS. Ugi 15 ♂ ad, 2 ♂ juv, 6 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 15 ♂ ad 94–117 (108·6) ; 2 ♂ juv 88, 92·5 ; 6 ♀ ad 94·5–109·5 (99·1). *Wing* 15 ♂ ad 128·5–134 (131·5) ; 2 ♂ juv 118, 122 ; 6 ♀ ad 122–129 (125·9). *Bill* 14 ♂ ad 19–20 (19·5) ; 2 ♂ juv 19, 20 ; 6 ♀ ad 18·5–20 (19·2).

Iris orange to orange-red, inner ring pale yellow (once golden-yellow) to pale green. *Skin* round eye pale blue-grey, eyelid pale yellow. *Bill* dark sage green basally, paler yellow-green distally, cere dull purple. *Foot* deep purple (bluish to reddish).

NOTES. Cain (1957) dismisses the character " malar apex concolorous with crown " (Ripley & Birckhead, 1942 : 8) as a mere form of words when applied to this grey-crowned species. However, the malar apex and the crown are pure grey, while the face and neck are washed with yellow. In individuals whose greys are exceptionally deep, the malar apex contrasts sharply with the paler and yellower face. It seems probable that the ancestral population did have the apex brightly coloured, like the crown—though this still further emphasizes the polyphyletic origin of the character.

(M. 29) *Ducula pacifica pacifica* (Gmelin, 1789)

REFERENCES. Amadon, 1943*a* : 10. See Goodwin, 1960.

RANGE. Small islands from Louisiades and Solomons to Polynesia.

NOTES. In the Solomons, the species is known from Buena Vista, Ramos, Gower, Sikaiana, Ongtong Java, Rennell (Amadon, 1943*a*), Bellona (Mayr, 1931*b*) and the Three Sisters (Cain & Galbraith, 1956 : 106 ; French, 1957). Only on the latter does it overlap with its close relative, *D. rubricera*.

(M. 30) **Ducula rubricera rufigula** (Salvadori, 1878)

REFERENCES. *Cat. Birds. B.M.* 21 : 179. See Goodwin, 1960.

RANGE. Solomons.

SPECIMENS. Guadalcanal : Betilonga 2 ♂ ad. San Cristoval : Goge 1 ? juv. 1 ♂ ad to OUM.

Wing 2 ♂ ad 240, 253. *Bill* 2 ♂ ad 33, 33·5.

Iris deep red or orange-red ; juv dark brown. *Skin* round eye blue-grey. *Bill* dark grey, base and cere cherry-red ; juv slaty-grey distally, grading to pale greyish-fawn base and cere. *Foot* purplish red (cherry-red in 1 of 5 ad), claws dark grey ; juv fawn, fuscous-tinged, claws grey.

Though small, the juvenile is as brightly-coloured as adults.

(M. 31) ***Ducula pistrinaria pistrinaria*** Bonaparte, 1855

REFERENCES. Hartert, 1926*a* : 34. See Goodwin, 1960.

RANGE. Feni, Nissan, Solomons (coasts).

SPECIMENS. Ugi 1 ♂ imm. To OUM.

Weight 390. *Wing* 220. *Tail* 130. *Bill* 29·5.

Iris dark brown. *Skin* round eye pale grey, eyelid reddish brown with blackish wash. *Bill* dark slate. *Foot* pinkish brown.

The specimen has faint juvenile barring on the breast, and is somewhat smaller than adults, with narrower rectrices. Oiliness of the plumage conceals any colour-difference.

(M. 32) ***Ducula brenchleyi*** (Gray, 1870)

REFERENCES. *Cat Birds B.M.* 21 : 225. See Goodwin, 1960.

RANGE. Eastern Solomons—Guadalcanal, Malaita, Ulawa, San Cristoval, Ugi, Three Sisters (mainly coasts ?).

SPECIMENS. Ugi 1 ♂ imm. To OUM.

Weight 380. *Wing* 210. *Tail* 105. *Bill* 31.

Iris reddish brown, inner ring yellowish brown. *Skin* round eye grey, eyelid greyish purple. *Bill* dark fuscous grey, tip black. *Foot* deep dull purplish-brown.

Like two juveniles from the Three Sisters, the specimen differs from adults in somewhat smaller size and narrower rectrices ; underparts less purplish (more rufous) brown, breast greyer and with pale barring, sides of breast grey not purplish, throat yellowish rather than pink.

NOTES. Though considered by Mayr (1945*a*) to be a forest bird, mainly of higher altitudes, this species is common on the coast of San Cristoval, especially in isolated trees, and also on the small islands of Ulawa, Ugi and the Three Sisters (Cain & Galbraith, 1956 : 123 ; French, 1957).

(M. 33) ***Gymnophaps solomonensis*** Mayr, 1931

REFERENCES. Mayr, 1931*f* : 11.

RANGE. Mountainous islands of the Solomons—Bougainville, Kolombangara, Vangunu, Guadalcanal, Malaita.

SPECIMENS. Guadalcanal : Betilonga 1 ♂ ad, 2 ♀ ad. 1 ♀ ad to OUM.

Weight 1 ♂ ad 385 ; 2 ♀ ad 310, 310. *Wing* 1 ♂ ad 226 ; 2 ♀ ad 221, 222. *Bill* 1 ♂ ad 29 ; 2 ♀ ad 25, 25·5.

Iris orange-red (1 ♂) or pinkish-orange (3 ♀) ; juv orange-red. *Skin* round eye, and eyelid, red (1 ♂) or reddish purple (2 ♀) ; juv blue-grey. *Bill* pale yellow, pinkish terminal or subterminal patch ; juv fuscous, tip pale. *Foot* lilac, pinkish in dried skin (1 ♂), or dull purplish-blue to dull lavender-grey, greyish in skins (3 ♀), claws fuscous ; juv dark grey.

(M. 34) ***Columba vitiensis halmaheira*** (Bonaparte, 1855)

REFERENCES. Amadon, 1943*a* : 14. See Goodwin, 1959.

RANGE. Moluccas, New Guinea region, Solomons.

Specimens. Guadalcanal : Turipava 2 ♂ ad. San Cristoval : Goge 1 ♂ ad, 1 ♀ ad. 1 ♂ ad to OUM.

Weight 1 ♂ ad 490 ; 1 ♀ ad 395. *Wing* 3 ♂ ad 219–229 (224·3) ; 1 ♀ ad 212. *Bill* 3 ♂ ad 29·5–31 (30·2) ; 1 ♀ ad 31.

Iris orange (yellowish to pinkish), inner ring brownish or greenish. *Skin* round eye maroon, more or less mixed with pale grey, eyelid dull reddish (brownish red to bluish purple). *Bill* ivory, base and cere dull reddish (pinkish red to bluish purple). *Foot* pinkish red, with back of shank bluer, to dull bluish purple, claws ivory.

(M. 35) *Columba pallidiceps* (Ramsay, 1877)

References. *Cat. Birds B.M.* 21 : 319 (*pallidiceps* + *philippana*) ; Mayr, 1934*a* : 4. See Goodwin, 1959.

Range. Bismarcks, Solomons.

Notes. Rare or retiring in the Solomons, but known from Guadalcanal and San Cristoval, and recorded by Ramsay (1882*a* : 722) from Ugi.

(M. 36) ***Macropygia mackinlayi arossi*** Tristram, 1879

References. *Cat. Birds B.M.* 21 : 363 (*rufocastanea*) ; Mayr, 1931*f* : 12.

Range. Nissan, Solomons, Rennell.

Specimens. Guadalcanal : Tenaru 1 ♀ ad ; Betilonga 1 ♀ juv ; Turipava 1 ♂ juv, 1 ♀ ad. San Cristoval : Goge 2 ♀ ad. 1 ♀ ad to OUM.

Weight 1 ♂ ad 79 ; 1 ♂ juv 91·5 ; 6 ♀ ad 79–88 (84·8) ; 1 ♀ juv 75. *Wing* 1 ♂ juv 138 ; 3 ♀ ad 137·5–142 (140·5) ; 1 ♀ juv 134·5. *Bill* 1 ♂ juv 18 ; 4 ♀ ad 17–18 (17·7) ; 1 ♀ juv 19·5.

Iris scarlet, sometimes irregularly mottled with yellow, inner ring yellow ; juv dull brown or pale brown. *Skin* round eye dark grey, eyelid grey or red. *Bill* black. *Foot* red (bright or dull, pinkish orange-red to crimson) ; juv fawn, toes fuscous.

The juveniles differ from adults in iris and foot colour (left and right irides seem to redden independently), and in more pointed rectrices, laxer plumage, and more black at the bases of the contour-feathers (yielding a scalloped pattern on the mantle).

(M. 37) ***Reinwardtoena crassirostris*** (Gould, 1856)

References. *Cat. Birds B.M.* 21 : 368 ; Mayr, 1944*c* : 1.

Range. Solomons.

Specimens. Guadalcanal : Betilonga 1 ♂ ad. To OUM.

Weight 2 ♂ ad 258, 260. *Wing* 208·5. *Bill* 26.

Iris yellow. *Skin* round eye deep red. *Bill* red basally, tip more orange. *Foot* red (purplish in 1 of 2).

Notes. In discussing the characters which separate this species from the representative *R. browni* and *R. reinwardtsi*, Mayr (1944*c*) inadvertently omits the most trenchant, the crest, which the others totally lack.

The species is known primarily from the larger islands of the Solomons, but also from Gatukai, Rendova, Ugi (Ramsay, 1882*c* : 36) and the Three Sisters. On the latter it rarely breeds, but is sometimes common (French, 1957).

(M. 38) ***Chalcophaps stephani mortoni*** Ramsay, 1881

REFERENCES. Rothschild & Hartert, 1901*b* : 189 ; Mayr, 1934*a* : 6.

RANGE. Nissan, Solomons (mainly lowlands).

SPECIMENS. Guadalcanal : Betilonga 1 ♂ juv. San Cristoval : Goge 3 ♂ ad. 1 ♂ ad to OUM.

Weight 3 ♂ ad 133·5–150 (143·8) ; 1 ♂ juv 87 ; 1 ♀ ad 132. *Wing* 3 ♂ ad 148–154 (150·0) ; 1 ♂ juv 110. *Bill* 3 ♂ ad 23·5–24 (23·8) ; 1 ♂ juv 22·5.

Iris dark brown ; juv brown. *Skin* round eye brownish grey to dull purple, eyelid dull purple. *Bill* deep purple basally, cere blackish ; distal 2/3 deep orange with bright yellow tip (3 ♂), or dull yellow separated from purple by blackish cross-streak (1 ♀) ; juv fuscous-brown, edges dull yellow. *Foot* cherry-red, toes more purplish ; juv dull pale purplish.

(M. 39) ***Gallicolumba beccarii solomonensis*** (Ogilvie-Grant, 1888)

REFERENCES. *Cat. Birds B.M.* 21 : 594 (*granti*) ; Mayr, 1931*b* : 12. See Hachisuka, 1931 ; Amadon, 1943*a*.

RANGE. Guadalcanal, San Cristoval Group, Gower, Rennell (lowlands).

SPECIMENS. San Cristoval : Goge 2 ♂ ad, 2 ? juv ; Nagasi 1 ♂ ad. 1 ♂ ad to OUM.

Weight 3 ♂ ad 93–98 (94·8). *Wing* 3 ♂ ad 105–106·5 (105·7). *Bill* 2 ♂ ad 18, 19.

Iris very dark brown. *Skin* round eye bluish white, eyelid dull yellow ; smaller juv dark grey round eye and under throat, wing and belly. *Bill* and cere black ; larger juv with yellowish tip, smaller fuscous, whitish distally with dark subterminal band and white tip (flexible in dried skin). *Foot* purplish red, toes bluer ; larger juv pinkish brown with somewhat fuscous toes, smaller pinkish fuscous-grey with back of shank flesh-colour.

(M. 40) *Gallicolumba jobiensis* cf. *chalconota* Mayr, 1935

REFERENCES. Mayr, 1936 : 2.

RANGE. Vella Lavella ; Guadalcanal (subspecies ?).

NOTES. Only four specimens are known from the Solomons : the adult male holotype from Vella Lavella, and three juveniles from Guadalcanal (*Cat. Birds B.M.* 21 : 599, footnote) one of which is in the BM(NH).

(M. 41) *Gallicolumba salamonis* (Ramsay, 1882)

REFERENCES. Ramsay, 1882*d* : 299.

RANGE. San Cristoval, Ramos.

NOTES. Only two specimens are known : the unsexed adult holotype from San Cristoval, and one from Ramos (Mayr, 1945*a*).

(M. 42) ***Caloenas nicobarica nicobarica*** (Linnaeus, 1758)

REFERENCES. Mayr, 1931*b* : 12.

RANGE. Malaysia to New Guinea region and Northern Melanesia.

SPECIMENS. Guadalcanal : above Tsea 1 ♀ ad. To OUM.

Wing 244. *Tail* 82. *Bill* 31.

Iris salmon pink. *Bill* and cere matt black. *Foot* purplish red, sole yellow.

(M. 44) ***Eos cardinalis*** (Gray, 1849)

References. *Cat. Birds B.M.* 20 : 22 ; Hartert, 1926*a* : 38 ; Auber, 1938 : 698. See Peters, 1935.

Range. Duke of York, Lavongai, Tabar, Lihir, Tanga, Feni, Nissan, Solomons (mainly lowlands).

Specimens. Guadalcanal : Tenaru 9 ♂ ad, 3 ♂ juv, 5 ♀ ad, 4 ♀ juv, 4 ? juv ; Betilonga 1 ♂ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 9 ♂ ad 173–205 (184·9) ; 4 ♂ juv 124–160 (145·4) ; 5 ♀ ad 168·5–195 (178·8) ; 4 ♀ juv 142·5–155 (148·4). *Wing* 4 ♂ ad 177–183 (180·7) ; 3 ♂ juv 166–173 (168·7) ; 4 ♀ ad 172·5–180 (175·4) ; 4 ♀ juv 165–171 (169·3). *Tail* 1 ♂ ad 154 ; 1 ♂ juv 116·5 ; 1 ♀ ad 150 ; 1 ♀ juv 144. *Bill* (from cere) 10 ♂ ad 20–22 (21·2) ; 4 ♂ juv 19·5–21 (20·1) ; 5 ♀ ad 20–21 (20·5) ; 4 ♀ juv 19·5–20 (19·6).

Iris orange-red to pinkish orange, very narrow black and yellow inner rings ; juv dull yellow. *Skin* round eye and under throat black, sharply-marked semi-circular yellow patch at base of mandible ; juv blackish or fuscous, irregularly mottled with more or less yellow. *Bill* reddish-orange, tip yellower, cere and base of maxilla black ; juv dull orange more or less suffused or mottled with blackish, especially towards cere. *Foot* black, ad sometimes with irregular patches of orange- to whitish-yellow.

The juveniles differ from adults in the coloration of their soft parts, especially that of the bare throat ; and in more pointed rectrices, more uniformly-coloured upperparts, ventral fringes yellower less white, and vaguer and whiter violet-blue areas at wing-bends and under wing-coverts. One BM(NH) juvenile from Guadalcanal has a much shorter tail, very wide yellow fringes ventrally, and conspicuously orange thighs.

The outer edges of the remiges and rectrices are subject to bleaching during life, turning from bronzy red to yellowish olive.

Notes. The generic placement of this species is obscure. Auber's (1938) intensive study associates it with the *atra-scintillata-duivenbodei* group of New Guinea, which Peters (1935) separates as *Chalcopsitta*, while Verheyen (1956) creates for it a monotypic genus *Cardeos*. Whereas Mayr (1941*a*) separates *Chalcopsitta* and *Pseudeos* from *Eos*, he later (1945*a*) includes *cardinalis* with the latter, thus giving to the unwary a false impression of the scope and range of the genus. His intention is clearly to adopt a broader generic concept for the Loriinae (as by following Amadon, 1942*b* in uniting *Charmosyna* with *Vini*), and to return all these forms to one genus. This seems the most acceptable solution until the subfamily has been critically revised.

(M. 45) ***Trichoglossus haematodus massena*** Bonaparte, 1854

References. Rothschild & Hartert, 1901*a* : 70 ; Cain, 1955 : 438, 445.

Range. Bismarcks to New Hebrides (lowlands).

Specimens. Guadalcanal : Tenaru 14 ♂ ad, 1 ♂ juv, 9 ♀ ad, 1 ♀ juv. San Cristoval : Goge 1 ♂ ad, 2 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight Guadalcanal 13 ♂ ad 83–103·5 (92·3) ; 1 ♂ juv 75·5 ; 9 ♀ ad 74·5–95·5 (84·9) ; 1 ♀ juv 82 ; San Cristoval 1 ♂ ad 117·5 ; 2 ♀ ad 97·5, 103. *Wing* Guadalcanal 10 ♂ ad 125–134 (130·9) ; 1 ♂ juv 130·5 ; 7 ♀ ad 122–132 (128·8) ; San Cristoval

1 ♂ ad 145 ; 2 ♀ ad 132, 135·5. *Tail* Guadalcanal 8 ♂ ad 96·5–104·5 (100·3) ; 1 ♂ juv 101·5 ; 5 ♀ ad 93–101 (97·1) ; 1 ♀ juv 86·5 ; San Cristoval 1 ♂ ad 101·5. *Bill* (from cere) 14 ♂ ad 18–20·5 (19·2) ; 1 ♂ juv 18 ; 10 ♀ ad 17–19·5 (18·4) ; 1 ♀ juv 17·5.

Iris orange-red (sometimes pinkish or dull, occasionally yellower or more scarlet) ; juv greyish yellow to pale dull brown. *Skin* round eye dark fuscous grey to black, throat whitish to pale flesh-colour with yellow tinge. *Bill* orange-red, tip yellower, cere dark fuscous grey to black ; juv dull orange streaked with blackish, especially distally. *Foot* fuscous-grey, more or less greenish or occasionally bluish.

The juveniles differ from adults in the colour of iris and bill (which in the dried skin is whiter basally), more pointed rectrices, and slight differences in plumage coloration—less blue and orange on the crown, no concealed red at the bases of feathers on the mid-back, more gradual transition from red breast to green belly, more evenly yellow-green thighs and under tail-coverts.

(M. 46) ***Lorius chlorocercus*** Gould, 1856

REFERENCES. *Cat. Birds B.M.* 20 : 38.

RANGE. Eastern Solomons—Guadalcanal, Savo, Malaita, Ulawa, San Cristoval, Ugi—and Rennell.

SPECIMENS. Guadalcanal : Betilonga 5 ♂ ad, 2 ♀ ad ; Turipava 1 ♂ ad. San Cristoval : Goge 1 ♀ ad ; Nagasi 1 ♂ ad. Ugi 4 ♂ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight Guadalcanal & San Cristoval 7 ♂ ad 168–185 (176·1) ; 4 ♀ ad 153–174·5 (160·6) ; Ugi 4 ♂ ad 190–225 (206·3). *Wing* Guadalcanal & San Cristoval 7 ♂ ad 160–174 (166·7) ; 3 ♀ ad 159–164 (161·0) ; Ugi 3 ♂ ad 176–181 (178·7). *Tail* Guadalcanal & San Cristoval 4 ♂ ad 89·5 –101·5 (95·4) ; Ugi 3 ♂ ad 95–100 (98·2) ; *Bill* (from cere) Guadalcanal & San Cristoval 6 ♂ ad 21·5–24 (22·7) ; 3 ♀ ad 21–22 (21·5) ; Ugi 4 ♂ ad 23–24·5 (22·1).

Iris dull orange to orange-red (Guadalcanal), pinkish-orange (San Cristoval and Ugi), inner ring yellow. *Skin* round eye black, throat white. *Bill* orange to reddish-orange, base of maxilla blackish, cere black. *Foot* dark grey, scutes black.

(M. 47) ***Vini meeki*** (Rothschild & Hartert, 1901)

REFERENCES. Rothschild & Hartert, 1901*b* : 187 ; Amadon, 1942*b* : 2.

RANGE. Higher islands of the Solomons—Bougainville, Kolombangara, Guadalcanal, Malaita (mainly mountains).

SPECIMENS. Guadalcanal : Betilonga 3 ♂ ad, 3 ♀ ad ; Turipava 1 ♂ ad, 2 ♀ ad. 1 ♂ ad to OUM.

Weight 4 ♂ ad 21–25·5 (24·1) ; 5 ♀ ad 21·5–25·5 (23·5). *Wing* 4 ♂ ad 78–81 (81·2) ; 5 ♀ ad 78–82 (80·4). *Tail* 3 ♂ ad 73–78·5 (75·0) ; 4 ♀ ad 64·5–70·5 (68·7). *Bill* (from cere) 4 ♂ ad 11·5–12 (11·7) ; 3 ♀ ad 10·5–11·5 (11·2).

Iris yellow to reddish orange. *Skin* round eye yellowish fuscous. *Bill* reddish orange, cere sometimes duller, mandible yellower, tip and edges blackish. *Foot* pale to reddish orange, claws fuscous.

(M. 49) *Vini margarethae* (Tristram, 1879)

References. *Cat. Birds B.M.* 20 : 81.

Range. Solomons.

Specimens. Guadalcanal : Tenaru 1 ♂ ad ; Betilonga 3 ♂ ad, 2 ♀ ad. San Cristoval : Goge 1 ♂ ad ; Nagasi 1 ♂ ad. 1 ♂ ad to OUM.

Weight 6 ♂ ad 52·5–59·5 (55·7) ; 2 ♀ ad 43, 44·5. *Wing* 5 ♂ ad 106·5–115 (111·7) ; 2 ♀ ad 108·5, 112. *Tail* 2 ♂ ad 95, 103 ; 2 ♀ ad 85·5, 101·5. *Bill* (from cere) 5 ♂ ad 14·5–15 (14·7) ; 2 ♀ ad 13·5, 14·5.

Iris orange, occasionally paler or duller. *Skin* round eye pale yellowish fuscous to black. *Bill* and cere orange, tip blackish. *Foot* orange, claws fuscous.

(M. 50) *Micropsitta finschii aolae* (Ogilvie-Grant, 1888)

References. Hartert, 1924*a* : 202.

Range. Guadalcanal, Florida and Russell Is., Malaita.

Specimens. Guadalcanal : Betilonga 5 ♂ ad, 2 ♂ juv, 1 ♀ ad, 1 ? juv. 1 ♂ ad to OUM.

Weight 5 ♂ ad 15–17·5 (15·9) ; 2 ♂ juv 14, 15·5 ; 1 ♀ ad 14·5. *Wing* 3 ♂ ad 62–66 (63·8) ; 2 ♂ juv 62, 63·5 ; 1 ♀ ad 59. *Tail* 4 ♂ ad 27·5–34 (31·4) ; 2 ♂ juv 30, 32 ; 1 ♀ ad 26. *Bill* (from cere) 5 ♂ ad 7·5–8 (7·8) ; 1 ♀ ad 7.

Iris ♂ orange ; ♀ and 1 juv dull yellow. *Skin* round eye grey. *Bill* ♂ blackish, whitish stripe under mandible, cere dull purplish red ; ♀ mottled horn, tip and base of maxilla darker, cere whitish ; juv as ♀ but cere pinkish or grey. *Foot* pale bluish grey.

(M. 50) *Micropsitta finschii finschii* (Ramsay, 1881)

References. Hartert, 1924*a* : 202.

Range. San Cristoval, Ugi, Rennell.

Specimens. San Cristoval : Manewiriwiri 2 ♂ ad ; Goge 3 ♀ ad ; Nagasi 2 ♂ ad, 1 ♀ ad. Ugi 3 ♂ ad, 1 ♀ ad.

Weight 8 ♂ ad 15·5–17·5 (16·6) ; 5 ♀ ad 14–18 (16·1). *Wing* 6 ♂ ad 62–67·5 (65·2) ; 5 ♀ ad 59–65·5 (63·0). *Tail* 6 ♂ ad 30·5–35·5 (33·3) ; 5 ♀ ad 27·5–32·5 (30·6). *Bill* (from cere) 5 ♂ ad 8–8·5 (8·3) ; 5 ♀ ad 7–8·5 (7·9).

Iris very dark brown (1 dull yellowish brown). *Skin* round eye blackish to pale grey. *Bill* ♂ slate, whitish stripe under mandible, cere pinkish grey to dull mulberry-red ; ♀ mottled bluish grey to horn, tip and sides of maxilla darker, cere dark grey (1 pinkish flesh). *Foot* pale bluish grey.

Though conspicuous in the intact males, the red belly-patch was lost or reduced during skinning.

(M. 51) *Micropsitta bruijnii rosea* Mayr, 1940

References. Mayr, 1940*b* : 2.

Range. Kolombangara, Guadalcanal (mountains).

Specimens. Guadalcanal : Turipava 1 ♂ ad.

Weight 14·5. *Wing* 65·5. *Tail* 28. *Bill* (from cere) 6·5.

Iris dark brown. *Skin* round eye fuscous. *Bill* grey, tip of maxilla and stripe under mandible white, tip of mandible yellowish. *Foot* grey.

(M. 52) ***Cacatua ducorpsii*** (Pucheran, 1853)

References. *Cat. Birds B.M.* 20 : 129. See Vane, 1959.

Range. Solomons except San Cristoval Group.

Specimens. Guadalcanal : Betilonga 3 ♂ ad. 1 ♂ ad to OUM.

Weight 3 ♂ ad 355–460 (408). *Wing* 3 ♂ ad 258–274 (264). *Tail* 2 ♂ ad 120, 121. *Bill* (from cere) 3 ♂ ad 32·5–34·5 (33·7).

Iris dark grey-brown. *Skin* round eye bright blue, throat grey to dull purplish. *Bill* pale horn, bluish at base. *Foot* black, greyish between scutes.

(M. 53) ***Larius roratus solomonensis*** (Rothschild & Hartert, 1901)

References. Rothschild & Hartert, 1901*a* : 82.

Range. Solomons.

Specimens. Guadalcanal : Betilonga 1 ♂ ad, 1 ♂ juv, 1 ♀ ad, 1 ♀ juv. Ugi 1 ♂ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 2 ♂ ad 370, 375 ; 1 ♂ juv 425 ; 1 ♀ ad 355 ; 1 ♀ juv 370. *Wing* 2 ♂ ad 245, 248 ; 1 ♂ juv 230 ; 1 ♀ ad 229 ; 1 ♀ juv 227. *Tail* 2 ♂ ad 109, 110·5. *Bill* (from cere) 2 ♂ ad 39, 40·5 ; 1 ♂ juv 37 ; 1 ♀ ad 36 ; 1 ♀ juv 34.

Iris ♂ orange ; ♀ yellow ; ♂ juv dull olive, ♀ juv brownish grey. *Skin* of throat straw-coloured. *Bill* ♂ maxilla orange, distal 1/3 golden-yellow, mandible black ; ♀ black ; juv black, tip of maxilla yellow or horn. *Foot* fuscous to dull black.

(M. 54) ***Geoffroyus heteroclitus heteroclitus*** (Hombron & Jacquinot, 1841)

References. *Cat. Birds B.M.* 20 : 412 ; Mayr, 1931*b* : 13.

Range. Bismarcks, Solomons (lowlands).

Specimens. San Cristoval : Goge 2 ? juv.

Iris very pale yellow, dull green inner ring. *Skin* round eye pale grey, eyelid dull yellow. *Bill* dull greyish horn, cere dull green. *Foot* dull greyish green.

(M. 55) *Cuculus saturatus* subspecies

Range. Eastern Palaearctic and Oriental regions, wintering in Malaysia and western Australasia.

Notes. Six specimens have been recorded from the Solomons, under various specific names : four from New Georgia (Rothschild & Hartert, 1905 : 258) and one each from Malaita (Mayr, 1931*f* : 13) and Ugi (Ramsay, 1882*c* : 21).

(M. 56) ***Cacomantis variolosus addendus*** Rothschild & Hartert, 1901

References. Amadon, 1942*b* : 20.

Range. Solomons.

Specimens. Guadalcanal : Tenaru 2 ♂ ad ; Betilonga 4 ♂ ad, 2 ♂ juv, 3 ♀ ad ; Turipava 2 ♂ ad. San Cristoval : Goge 2 ♂ ad. 1 ♂ ad. to OUM.

Weight Guadalcanal 9 ♂ ad 38–45·5 (42·4) ; 2 ♂ juv 38, 39 ; 3 ♀ ad 38–42·5 (40·0) ; San Cristoval 2 ♂ ad 35·5, 38. *Wing* Guadalcanal 7 ♂ ad 121–131 (124·4) ; 2 ♂ juv 113·5, 115 ; 3 ♀ ad 110·5–112 (111·2) ; San Cristoval 2 ♂ ad 116, 121. *Tail*

Guadalcanal 2 ♂ ad 139, 139; 2 ♂ juv 106, 124·5; 1 ♀ ad 141; San Cristoval 1 ♂ ad 141. *Bill* Guadalcanal 8 ♂ ad 19–20 (19·5); 2 ♂ juv 17, 18·5; 2 ♀ ad 19, 20; San Cristoval 2 ♂ ad 19, 20.

Iris dark reddish brown, wholly or partly ringed with white. *Eyelid* yellow (bright to dull and greenish). *Bill* maxilla black, mandible horn-colour more or less mottled with fuscous and yellowish, gape yellow to pale grey externally, orange-red internally. *Foot* yellow (orange-yellow to pale and dull) more or less tinged with greyish or fuscous, claws fuscous or blackish.

One female, with much enlarged ovarian follicles, has the throat to the upper belly barred with dark subterminal chevrons. This is clearly a somewhat retarded plumage, seen also in a short-tailed subadult female in the BM(NH) (recorded by Ogilvie-Grant, 1888 : 191 as *tymbonomus*), and in a female from Bougainville, probably immature, in the AMNH (P. Vaurie, *in litt.*).

(M. 57) ***Cacomantis pyrrhophanus pyrrhophanus*** (Viellot, 1817)

References. Amadon, 1942*b* : 16.

Range. New Caledonia and Loyalty Is.; partial migrant, occasionally wintering in Solomons.

Specimens. Guadalcanal : Tenaru 1 ♂ ad.

Weight 56·5. *Wing* 140. *Tail* 148·5. *Bill* 22·5.

Iris bright red-brown. *Eyelid* dull yellow. *Bill* maxilla black, mandible grey mottled with darker grey and yellow, gape pale flesh-colour externally, pinkish orange internally. *Foot* dull yellow tinged with fuscous, claws dark fuscous.

Notes. Four other specimens are recorded from the Solomons : three from Ysabel (Rothschild & Hartert, 1902 : 587) and one from Bellona (Mayr, 1931*b* : 14).

(M. 58) ***Chrysococcyx lucidus lucidus*** (Gmelin, 1788)

References. Mayr, 1932*b* : 2.

Range. New Zealand, Chatham, Norfolk (and Lord Howe ?) Is.; migrant, wintering in Northern Melanesia.

Specimens. Guadalcanal : Tenaru 2 ♂ ad ; Betilonga 1 ♂ ad. 1 ♂ ad to OUM.

Weight 3 ♂ ad 21·5–27 (24·4). *Wing* 3 ♂ ad 103–104·5 (103·7). *Tail* 3 ♂ ad 68·5–70 (69·2). *Bill* 3 ♂ ad 18–19·5 (18·5). *Bill width* (at front of nostril) 3 ♂ ad 5·5–6 (5·8).

Iris dark brown to grey-brown. *Eyelid* whitish. *Bill* black, base of mandible silvery to dark grey. *Foot* bluish grey, sole pale yellowish.

Notes. We follow Berger (1955), who shows that *Chalcites* cannot be separated from *Chrysococcyx* and *Lampromorpha*.

Since Mayr's (1932*b*) summary of records, White (1938) and Baker (1948) have recorded this race from Bougainville, in May and September. As Mayr conjectured, one of the specimens recorded by Tristram (1882) as *plagosus* actually belongs to *lucidus* (Russell Is., 24th September, 1880). Another BM(NH) specimen (Bouin, Bougainville, 25th November, 1938, W. F. H. Rosenberg) was taken long after the migrants normally return to New Zealand (Mayr, 1932*b* ; Fell, 1947).

Three of Mathews' specimens from Norfolk Island support his statement (1918 :

352) that *lucidus* breeds there: an adult female (2nd December, 1912) is labelled " this bird would also have laid tomorrow "; and there are two juveniles (20th and 23rd January, 1913), one labelled " was fed by No. 536 " (the identity of which cannot be traced). Despite Mayr's (1932*b* : 5) view that this race does not migrate through Southern Melanesia, a juvenile from New Caledonia (Ausevata, 26th April, 1877, E. L. Layard) belongs to it, and not to the resident *layardi*.

(M. 58) ***Chrysococcyx lucidus plagosus*** (Latham, 1801)

REFERENCES. Mayr, 1932*b* : 6.

RANGE. Tasmania and southern Australia; migrant, wintering from northern Australia to Lesser Sunda Isles and Northern Melanesia.

SPECIMENS. Guadalcanal: Betilonga 1 ♂ ad, 2 ♀ ad.

Weight 1 ♂ ad 21; 2 ♀ ad 21·5, 23. *Wing* 1 ♂ ad 89·5; 2 ♀ ad 95·5, 95·5. *Tail* 1 ♂ ad 65·5; 1 ♀ ad 68. *Bill* 1 ♂ ad 18·5; 1 ♀ ad 19·5. *Bill width* (at front of nostril) 1 ♂ ad 4; 2 ♀ ad 4·5, 5.

Iris dark brown to fawn. *Bill* black, base of mandible whitish to pale grey. *Foot* bluish grey, sole pale yellow.

Two of these specimens agree in all respects with Australian *C. l. plagosus*, except that their upper throats and chins are white with only a trace of barring. They have been compared with the specimens of *plagosus* at the AMNH by Mrs. Vaurie (*in litt.*), and at the BM(NH). The third specimen, a female, has more white and green on the head than most of those from Australia, but falls within their range of variation. It is damaged, but has the stump of the bill conspicuously narrow.

NOTES. It is not surprising that this race should prove to winter in the Solomons, despite Mayr (1932*b* : 3), since both *lucidus* and *plagosus* are known from the Bismarcks (see Mayr, 1941*a* : 73). An adult male from Guadalcanal (recorded by Ogilvie-Grant, 1888 as *C. basalis*) belongs to this race.

(M. 59) ***Eudynamis scolopacea alberti*** Rothschild & Hartert, 1907

REFERENCES. Rothschild & Hartert, 1907 : 440; 1908*a* : 356.

RANGE. Solomons (lowlands).

SPECIMENS. Guadalcanal: Tenaru 1 ♀ ad. San Cristoval: Goge 1 ♂ ad.

Weight 1 ♂ ad 190; 1 ♀ ad 148. *Wing* 1 ♂ ad 185; 1 ♀ ad 179. *Tail* 1 ♂ ad 197; 1 ♀ ad 207·5. *Bill* 1 ♂ ad 30; 1 ♀ ad 29.

Iris ♂ bright crimson; ♀ light rufous-brown. *Bill* ♂ greenish silvery grey, base and tip of maxilla black; ♀ dark horn, gape and mandible light greenish-tinged horn. *Foot* greenish grey, toes fuscous.

(M. 60) *Eudynamis taitensis* (Sparrman, 1787)

REFERENCES. Bogert, 1937 : 1; Mayr, 1944*c* : 1.

RANGE. New Zealand; migrant, wintering in Polynesia and more rarely in Southern and Northern Melanesia and Micronesia.

NOTES. Bogert (1937) records 18 specimens from the Solomons, mainly from small outlying islands. No further specimens have been recorded, but French (1957) reports the species as common in the Three Sisters.

(M. 61) ***Centropus milo milo*** Gould, 1856

REFERENCES. *Cat. Birds B.M.* 19 : 335 ; Rothschild, 1904 : 59.

RANGE. Guadalcanal, Florida Is.

SPECIMENS. Guadalcanal : Betilonga 2 ♂ ad, 1 ♂ imm, 1 ♀ ad, 1 ? juv. 1 ♂ ad to OUM.

Wing 2 ♂ ad 270, 272 ; 1 ♀ ad 265. *Bill* 2 ♂ ad 63·5, 64 ; 1 ♂ imm 57·5 ; 1 ♀ ad 63·5.

Iris dark brownish red ; imm and juv grey. *Skin* round eye and at base of bill dark grey. *Bill* black, whitish streaks under mandible ; imm and juv maxilla grey-brown to dark fuscous, mandible pale horn whitish below. *Foot* silvery blue-grey.

An immature and a juvenile in the BM(NH) agree with ours in showing that the dull black plumage of the foreparts, though not loose in texture, belongs to the same feather-generation as the barred loose juvenile plumage of the hinderparts. It is replaced by immature feathers which have large subterminal spots and bars, rufous above and whitish below, with a much paler appearance (cf. Cain & Galbraith, 1956 : 132). The immature plumage of the hinderparts is similar in coloration, though not in texture, to the juvenile plumage which it replaces. Variation in the colour of the quills and their bars, and in the width and definition of the bars, seems to be merely individual.

(M. 62) *Tyto alba* cf. *crassirostris* Mayr, 1935

REFERENCES. Mayr, 1936 : 10.

RANGE. Tanga, Nissan, Solomons and Rennell Group ; geographical variation not yet understood.

NOTES. Only four specimens are known from the Solomons proper—from Vella Lavella, New Georgia, Malaita and Santa Ana—besides the topotypical series from Boang (Tanga group near New Ireland), two specimens from Nissan, and one from Bellona (Mayr, 1936 ; Sibley, 1951 ; Bradley, 1962). However, the species is apparently not uncommon on New Georgia (Sibley, 1951). It is also known from sight-records on the Three Sisters, as a rare non-breeding visitor (French, 1957), and on Rennell (Bradley & Wolff, 1956)—where, as on Guadalcanal, San Cristoval and Ugi (Cain & Galbraith, 1956), it is known to the natives.

The inadequate material from Nissan and the Solomons, tentatively assigned to this race by Mayr (1936), suggests considerable geographical variation without revealing its pattern. In coloration, these specimens agree generally with topotypical *crassirostris*, with *delicatula* of Australia, and with *lulu* of Central Polynesia ; and are distinct from the pale *meeki* of south-eastern New Guinea and the ventrally ochraceous *interposita* of northern Southern Melanesia. These forms are reviewed by Mayr (1936) and Amadon (1942*b*). Topotypical *crassirostris* differs from *delicatula* in its much deeper bill, larger size, richer ochraceous and darker grey upper parts, broader and darker barring on tail and wing, and somewhat bolder spotting above and below. Four specimens from the Solomons and Nissan are intermediate in dimensions, and one from Santa Ana agrees rather with *delicatula*, while they span the range of coloration between the two races. While *lulu* averages still smaller and still less ochraceous above than *delicatula*, they overlap in both coloration and dimensions.

Bradley (1962) describes as a new race, *bellonae*, a specimen recently collected on Bellona. This she compares with the somewhat inadequate material of *delicatula*, *lulu*, *meeki* and *interposita* in the BM(NH). She mentions the size of topotypical *crassirostris*, given in Mayr's original and scarcely more than nomenclaturally valid description (1935), but does not quote Mayr (1936) nor Amadon (1942*b*). I.C.J.G. has compared the type of *bellonae* with a paratype of *crassirostris*, with specimens from Nissan and Santa Ana, and with the BM(NH) material. Measurements of both sexes are combined in quoting (within square brackets) those extracted from Mayr and Amadon, since there is apparently no sexual dimorphism even in mean dimensions; though in fact the four critical specimens are all females. In the following discussion *bellonae* refers to the type, *crassirostris* to the topotypical series.

Wing-length. In many of the specimens examined, the metacarpo-phalangeal joint distal to the wing-bend is flexed, to a degree that more or less seriously reduces the measured wing-length. This flexure was especially marked in *bellonae*, so that after freeing the joint it is possible to obtain a measurement 15 mm greater than that taken by Bradley. The value given here was taken with the joint somewhat flexed, for comparison with the other specimens: *bellonae* 282, Santa Ana 274 [273]; Malaita & Vella Lavella [279, 283]; Nissan, ♀ 283 [281], ♂ [288]; *crassirostris* 291 [285–290 (287·8)]; *delicatula* [273–291 (284)]; *lulu* [262–282 (272)].

Tail-length. Bradley clearly measured the tail from a different basal point, giving a much higher value than those obtained by Mayr and Amadon, and (in combination with the unduly low wing value) yielding a tail/wing ratio of 45%; whereas Mayr and Amadon's mean figures yield ratios between 40% and 41%. The corrected measurements for *bellonae* yield a ratio of just under 40%. In order to obtain the same values as Mayr from the same specimens, the tails were measured from the common sheath of the central rectrices to the tip of the longer second rectrix, the central pair being shorter and variably developed: *bellonae* 112; Santa Ana 109 [109]; Malaita & Vella Lavella [112, 115]; Nissan, ♀ 113 [113], ♂ [113]; *crassirostris* 116 [113–116 (114·8)]; *delicatula* [109–120 (114)]; *lulu* [105–119 (112)].

Maxilla-depth. This character, on which Mayr assigned the Nissan and Solomons specimens to " *crassirostris* ", is not mentioned by Bradley. Since *bellonae* has the culmen damaged at the cere, it has been necessary to take this measurement slightly further forward, perpendicular to the tomium just in front of its obtuse angle, across the front edge of the nostril. This method, probably less reliable, yields measurements approximately 0·2 mm. less than Mayr and Amadon's, which are here adjusted by that amount: *bellonae* 9·3; Santa Ana 9·5 [9·4]; Malaita & Vella Lavella [10·4, 10·5]; Nissan, ♀ 10·5 [10·5], ♂ [9·9]; *crassirostris* 11·0 [10·8–11·1 (10·9)]; *delicatula* [8·3–10·0 (9·1)]; *lulu* [8·2–9·8 (9·1)].

Coloration. The female from Nissan and *crassirostris* differ from the specimens of *delicatula* and *lulu*, and that from Santa Ana, in having the distal white spots on the mantle feathers reduced and the proximal white bars somewhat widened. This trend is carried furthest in *bellonae*, in which the large black spots are margined by subequal white bars proximally and distally. The feathers defining the facial disc have unusually small black tips in *bellonae*, but this condition is paralleled in a few specimens of *lulu* and *delicatula*, and seems to be due in part to wear of the tips. The purer and darker greys, especially on the head, of *bellonae* are certainly due to foxing of the other specimens, of which the most recent (*crassirostris*) was taken twenty-four years earlier ; while the same is probably true of its deeper blacks. In its rich ochraceous areas on the upper parts, *bellonae* agrees with *crassirostris*, while the bars on its tail and wings are intermediate in width, as in the Nissan and Santa Ana specimens.

It seems probable that the next revision of these populations will result in a single variable race (*delicatula*) in Australia, Northern Melanesia and Central Polynesia (whether or not a broader subspecies-concept finally results in further combination). The data on *lulu* and *delicatula* given by Amadon are suggestive, but inadequate to determine the statistical separation of the populations according to the " 75% rule " or a variant (see Amadon, 1949). Only the differences in wing and tail lengths are put forward to justify separation, and it seems improbable that the statistics for the latter (difference between means 2 mm, spreads of samples 14 & 11 mm, overlap between samples 10 mm) conceal sufficiently separated distributions. Only the provision of standard deviations or related statistics could have shown whether the wing-length distributions (for which the corresponding values are 12, 20 & 18, and 9 mm) were separable. While topotypical *crassirostris* seems amply distinct from *delicatula* according to current standards, the few other Northern Melanesian specimens already reveal inextricable intermediacy. However, it seems best to maintain the accepted nomenclature pending a full revision, while emphasizing the heterogeneity of " *crassirostris* ". Only the pattern of the dorsal spots could conceivably justify the separation of *bellonae*, and much more material from Northern Melanesia is necessary to determine the constancy and importance of this character.

(M. 63) ***Ninox jacquinoti granti*** Sharpe, 1888

REFERENCES. Sharpe, 1888 : 183.

RANGE. Guadalcanal.

SPECIMENS. Guadalcanal : Turipava 1 ♂ ad, 1 ♀ ad. 1 ♂ ad to OUM.

Weight 1 ♂ ad 153·5 ; 1 ♀ ad 158. *Wing* 1 ♂ ad 173 ; 1 ♀ ad 182. *Tail* 1 ♀ ad 95. *Bill* 1 ♂ ad 25·5 ; 1 ♀ ad 26.

Iris yellow. *Bill* dirty greenish yellow, more fuscous at base ; cere ♂ greenish yellow, ♀ greenish fuscous. *Foot* pale dirty yellow, fuscous-tinged, claws fuscous.

(M. 63) ***Ninox jacquinoti roseoaxillaris*** (Hartert, 1929)

REFERENCES. Hartert, 1929 : 6.

RANGE. San Cristoval.

SPECIMENS. San Cristoval : Goge 1 ♂ ad.

Weight 147. *Wing* 150·5. *Tail* 82·5. *Bill* 25·5.

Iris brownish grey. *Bill* greenish straw-colour, whitish blue-grey basally, cere pale fleshy grey mottled with blackish. *Foot* dull whitish yellow, claws dark grey.

This is probably the third known specimen, Ramsay's (1883 : 672) " *Ninox taeniata* ? juv." being the first. Dr. Amadon finds that it agrees with the holotype, except in being slightly more conspicuously marked with white on wing-coverts and hind-neck, and in a stronger suggestion of barring on the mid-abdomen (P. Vaurie, *in litt.*).

The porphyrin pigment which gives the characteristic pink tinge to the under wing-coverts and axillaries of this species fluoresces brilliantly under ultra-violet illumination. The pigment is generally distributed in the dark bases of the body-feathers in many *Ninox* and other owls, but forms clear patches only under the wings. The extent of the fluorescent patches in *N. jacquinoti* may be of systematic significance. In 4 specimens of *eichhorni*, 5 of *jacquinoti* and 8 of *granti* it extends to the wing-bend ; whereas in this specimen of *roseoaxillaris* a broad area within the bend is without porphyrin, showing white under the UV lamp. However, in a ninth specimen of *granti* this area shows little fluorescence. The fluorescence is faint in some of the older skins, and UV examination of longer series of fairly fresh specimens will be necessary to determine the constancy of this character.

(M. 67) *Collocalia whiteheadi orientalis* Mayr, 1935

REFERENCES. Mayr, 1936 : 12.

RANGE. Guadalcanal (mountains ?).

NOTES. Only the holotype is known.

(M. 68) ***Collocalia vanikorensis vanikorensis*** (Quoy & Gaimard, 1830)

REFERENCES. Mayr, 1937 : 4.

RANGE. New Hebrides to Solomons and ? Bismarcks; minor geographical variation.

SPECIMENS. San Cristoval : Goge 1 ♂ ad. Ugi 2 ♂ ad. 1 ♂ ad to OUM.

Weight 3 ♂ ad 9–11·5 (10·5). *Wing* 3 ♂ ad 113–115·5 (114·7). *Tail* 2 ♂ ad (inner) 44, 45 ; (outer) 54, 54·5. *Bill* 3 ♂ ad 8·5–9 (8·7).

Iris very dark brown. *Bill* black. *Foot* fuscous grey, shanks purplish, fleshy above, toes blackish.

NOTES. In addition to the islands in the Solomons listed by Mayr (1937), the species is known from Malaita (Davidson, 1934 : 193), San Cristoval and the Three Sisters (Cain & Galbraith, 1956 : 133, 106), and from Rennell (Bradley & Wolff, 1956 : 102).

(M. 69) ***Collocalia spodiopygia reichenowi*** Stresemann, 1912

REFERENCES. Streseman, 1912 : 350 ; Hartert, 1924*b* : 269 ; Mayr, 1937 : 16.

RANGE. Solomons, Rennell.

SPECIMENS. San Cristoval : Goge 1 ♂ ad. Ugi 1 ♂ ad.

Weight 2 ♂ ad 7, 8·5. *Wing* 2 ♂ ad 103, 105. *Tail* 2 ♂ ad (inner) 41, 41 ; (outer) 47, 49·5. *Bill* 1 ♂ ad 8.

Iris very dark brown. *Bill* black. *Foot* fuscous (1 very pale), toes blackish.

NOTES. Formerly known only from Guadalcanal and Kolombangara (Stresemann, 1912 ; Mayr, 1945*a* : 239), but now also from San Cristoval and Ugi (Cain & Galbraith, 1956 : 133) and Rennell (Bradley & Wolff, 1956 : 102). In these localities at least, it is not confined to the mountains.

(M. 70) ***Collocalia esculenta becki*** Mayr, 1931

References. Mayr, 1931*b* : 16.

Range. Solomons except San Cristoval Group.

Specimens. Guadalcanal : Betilonga 1 ♂ ad. To OUM.

Weight 7·5. *Tail* inner 39 ; outer 42. *Bill* 6·5.

Iris dark brown. *Bill* black. *Foot* pinkish grey, claws fuscous.

Notes. Recorded from Malaita by Mayr & Camras (1938).

(M. 70) ***Collocalia esculenta makirensis*** Mayr, 1931

References. Mayr, 1931*b* : 15.

Range. San Cristoval, Three Sisters, ? Ugi.

Specimens. San Cristoval : Goge 1 ♂ ad ; Nagasi 2 ♂ juv, 2 ♀ ad, 1 ? juv. 1 ♀ ad to OUM.

Weight 1 ♂ ad 5 ; 2 ♂ juv 5·5, 6·5 ; 1 ♀ ad 5·5. *Wing* 1 ♂ ad 87 ; 2 ♀ ad 93, 93. *Tail* (inner) 1 ♂ ad 39·5 ; 2 ♀ ad 39, 41 ; (outer) 1 ♂ ad 41 ; 2 ♀ ad 44, 44·5. *Bill* 1 ♂ ad 6·5 ; 2 ♀ ad 6, 6.

Iris very dark brown. *Bill* black. *Foot* purplish grey, pale to blackish, claws black ; juv pale, dull flesh to grey, with purplish tinge.

Notes. Two BM(NH) specimens recorded from Ugi (Gray, 1873) carry field labels showing them to have been collected there by Brenchley, and belong to this race. The species has not recently been taken on Ugi (Mayr, 1945*a* : 279) and seems not to be present (Cain & Galbraith, 1956 : 104).

(M. 71) ***Hemiprocne mystacea woodfordiana*** (Hartert, 1896)

References. Hartert, 1896 : 19 ; Stresemann, 1921 : 38.

Range. Feni, Solomons, Rennell (lowlands).

Specimens. Guadalcanal : Nala 1 ♀ ad, 1 ♀ imm. 1 ♀ imm to OUM.

Weight 1 ♀ ad 59·5 ; 1 ♀ imm 53. *Wing* 1 ♀ ad 202. *Tail* 1 ♀ ad (inner) 58·5 ; (outer) 185. *Bill* 1 ♀ ad 16·5 ; 1 ♀ imm 16·5.

Iris dark brown. *Skin* round eye and gape purplish grey. *Bill* black. *Foot* blackish, legs purplish.

(M. 72) ***Alcedo atthis salomonensis*** Rothschild & Hartert, 1905

References. Rothschild & Hartert, 1905 : 255 ; 1908*b* : 361 (*ispida* subsp.) ; Stresemann, 1913 : 316.

Range. Solomons ; irregular geographical variation, some populations scarcely distinct from *A. a. hispidiodes* (mainly lowlands).

Specimens. San Cristoval : Goge 1 ♂ imm, 1 ♀ imm. 1 ♀ imm to OUM.

Weight 1 ♂ imm 35 ; 1 ♀ imm 35·5. *Wing* 1 ♂ imm 73 ; 1 ♀ imm 74. *Tail* 1 ♂ imm 33·5 ; 1 ♀ imm 32·5. *Bill* (from front of nostril) 1 ♂ imm 31 ; 1 ♀ imm 31·5.

Iris very dark brown. *Bill* black ; ♂ gape dull pinkish fuscous, pale salmon-pink internally ; ♀ gape dull orange, base of mandible dull orange. *Foot* orange-red with fuscous wash, especially on toes.

(M. 73) *Ceyx pusillus aolae* (Ogilvie-Grant, 1914)

References. Ogilvie-Grant, 1914 : 13.

Range. Guadalcanal, Florida Is. (coasts).

Notes. This mangrove-living species is known by only a few specimens from any island in the Solomons, and though it has not yet been recorded from San Cristoval or Malaita it may still be found there.

(M. 74) ***Ceyx lepidus nigromaxilla*** Rothschild & Hartert, 1905

References. Rothschild & Hartert, 1905 : 256 ; Mayr, 1936 : 5.

Range. Guadalcanal.

Specimens. Guadalcanal : Betilonga 3 ♂ ad, 1 ♀ ad ; Tasinasa, near Nala, 1 ♀ ad ; Turipava 1 ♂ ad. 1 ♂ ad to OUM.

Weight 3 ♂ ad 19–19·5 (19·2) ; 2 ♀ ad 19, 20·5. *Wing* 4 ♂ ad 57·5–59·5 (58·8) ; 2 ♀ ad 60, 62. *Tail* 4 ♂ ad 23·5–25·5 (24·8) ; 2 ♀ ad 25, 25. *Bill* (from front of nostril) 4 ♂ ad 29–30·5 (29·8) ; 1 ♀ ad 30·5.

Iris dark brown. *Bill* maxilla black, more or less streaked with dull orange, mandible orange-red streaked with black at tip and sometimes towards base. *Foot* orange to orange-red.

The small weight (16·5) of one male from Betilonga is not listed above, since the bird was evidently starved : it was caught by hand, and found to have one wing hampered by sticky fruit.

(M. 74) ***Ceyx lepidus gentianus*** Tristram, 1879

References. Tristram, 1879 : 438.

Range. San Cristoval.

Specimens. San Cristoval : Goge 3 ♂ ad, 2 ♀ ad, 1 ♀ juv, 1 ? juv ; Nagasi 2 ♀ ad. 1 ♀ ad to OUM.

Weight 3 ♂ ad 24·5–28 (26·8) ; 4 ♀ ad 27–29·5 (28·4) ; 1 ♀ juv 25. *Wing* 3 ♂ ad 61·5–64 (62·5) ; 4 ♀ ad 63–65 (64·4). *Tail* 3 ♂ ad 27·5–28·5 (28·0) ; 3 ♀ ad 29–31 (30·2). *Bill* 3 ♂ ad 31·5–33 (32·2) ; 4 ♀ ad 29–31 (29·9) ; 1 ♀ juv 19.

Iris very dark brown ; juv very dark grey-brown. *Bill* black, gape greyish to brownish fuscous ; juv tip white. *Foot* orange ; juv pale pinkish flesh.

The juveniles (which have growing quills, and white overhanging tips to their bills) were taken from a nest hole, by a native collector who had seen them flying.

(M. 75) ***Halcyon chloris alberti*** Rothschild & Hartert, 1905

References. Hartert, 1926*b* : 132 ; Mayr, 1936 : 6.

Range. Solomons, except Russell Is., Malaita and San Cristoval Group : very similar to *H. c. tristrami*.

Specimens. Guadalcanal : Tenaru 3 ♂ ad, 1 ♂ juv, 2 ♀ ad, 1 ? juv ; Betilonga 2 ♂ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 5 ♂ ad 73·5–82·5 (76·8) ; 1 ♂ juv 70 ; 2 ♀ ad 77, 77·5. *Wing* 5 ♂ ad 104·5–110·5 (107·3) ; 1 ♂ juv 106·5 ; 2 ♀ ad 104·5, 105·5. *Tail* 4 ♂ ad 64–68 (65·4) ; 1 ♂

juv 67 ; 2 ♀ ad 67, 69·5. *Bill* (from front of nostril) 5 ♂ ad 37–39 (38·2) ; 1 ♂ juv 33 ; 2 ♀ ad 38·5, 41.

Iris dark brown ; 1 juv dark grey-brown. *Bill* black, basal half of mandible ivory, sometimes pinkish ; juv tip ivory, gape pale grey, base brownish. *Foot* fuscous black.

(M. 75) ***Halcyon chloris solomonis*** Ramsay, 1882

References. Hartert, 1926*b* : 132.

Range. San Cristoval Group, except Three Sisters.

Specimens. San Cristoval Manewiriwiri 1 ♂ ad ; Goge 19 ♂ ad, 8 ♀ ad, 5 ♀ imm. Ugi 12 ♂ ad, 1 ♂ juv, 18 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight San Cristoval 17 ♂ ad 47·5–61 (57·4) ; 7 ♀ ad 61–71·5 (65·0) ; 5 ♀ imm 57–66 (61·5) ; Ugi 12 ♂ ad 54–62·5 (56·5) ; 1 ♂ juv 58·5 ; 18 ♀ ad 57–69·5 (62·9). *Wing* San Cristoval 20 ♂ ad 89·5–96 (92·7) ; 6 ♀ ad 93–95·5 (94·4) ; 5 ♀ imm 90·5–94 (92·2) ; Ugi 9 ♂ ad 92·5–96 (94·7) ; 1 ♂ juv 92 ; 15 ♀ ad 90–100 (94·8). *Tail* San Cristoval 19 ♂ ad 59–66·5 (63·1) ; 6 ♀ ad 63–67·5 (64·7) ; 5 ♀ imm 62–64 (62·8) ; Ugi 9 ♂ ad 61–65 (63·4) ; 12 ♀ ad 59·5–68·5 (66·0). *Bill* (from nostril) San Cristoval 20 ♂ ad 34·5–39 (37·1) ; 8 ♀ ad 37·5–40·5 (38·5) ; 5 ♀ imm 36·5–40·5 (38·0) ; Ugi 12 ♂ ad 33·5–38·5 (36·7) ; 1 ♂ juv 32·5 ; 18 ♀ ad 33·5–40·5 (38·5).

Iris dark to very dark brown (1 dark grey-brown). *Bill* black, base of mandible white to very pale grey, sometimes pinkish ; juv base of mandible dull grey. *Foot* blackish, shank purplish.

As Ramsay (1882*b* : 834) points out, the pale supraloral spots, which are the remnants of the " ringband " (Mayr, 1931*a* : 3) in this race, are sometimes still further reduced to vanishing-point. This tendency seems to be confined to Ugi, whence 11 of our 31 specimens (6 ♂, 5 ♀) have the spots obsolete or lacking. All 33 specimens from San Cristoval (and the one from Santa Ana at the AMNH—P. Vaurie, *in litt.*) have the spots well developed, extending back as more or less concealed superciliary stripes. Indeed, one male from Goge (BM(NH) reg. no. 1959.21.329) has a well-developed though concealed ring-band connecting the superciliaries across the nape ; although the ochraceous area is subterminal on most of the nape feathers, a few are pale to the tip.

There are also striking differences, in the mean values of several colour characters, between the San Cristoval and Ugi series, with the former much the more variable. This is most conspicuous in the coloration of the male underparts, which are predominantly rufous in many San Cristoval specimens but mainly white in the Ugi series. However, plotting colour-classes against collection-dates shows a progressive paling, superimposed on great variation at any one time, during eight weeks on San Cristoval ; and suggests that the more uniform palor of the Ugi series (collected in two weeks) may result merely from the continuance of this trend. Like the bleaching of phaeomelanin, most of the other colour characters which vary in these series are known to be affected by wear (Mayr, 1931*a* : 3). In each the San Cristoval series is the more variable, while the mean displacement of the Ugi series is towards the worn condition : head bluer, mantle less blackish green, less dark fringing on sides of breast, female underwing less ochraceous.

The impression given by the present series, that *solomonis* is unusual among the races of *H. chloris* in its susceptibility to wear and consequent variability, needs confirmation on fresher specimens. Intergradation from pale to dark ochraceous also appears unusually abrupt on the underparts of the most deeply-coloured males, though the effect may be exaggerated by the make-up of the skins. The rufous is most intense at the sides of the breast, between which the paler mid-breast contrasts sharply with the large white throat-patch and intergrades with the still paler belly; but the field impression is not of an interrupted ochraceous gorget (cf. Rothschild & Hartert, 1908*b* : 361; Hartert, 1926*b* : 132; Mayr, 1945*a* : 243).

The 5 female immatures from Goge (collected 2nd–12th November, ovaries enlarged, 1 with oocytes c. 3 mm diam.) do not have the short bills with white overhanging tips, nor the deeply ochraceous and strongly-fringed underparts, characteristic of juveniles. However, they show the juvenile characters of buffy under wing-coverts, buff edges to the upper wing-coverts, a little buff in the forehead, and somewhat more olivaceous upperparts. No comparable stage is distinguishable in the other series: 3 males from Goge have some buff in the upper wing-coverts, but no other juvenile characters.

(M. 75) *Halcyon chloris sororum* **new subspecies**

HOLOTYPE. British Museum (Natural History) reg. no. 1940.7.4.17. ♂ adult, Malau Paina Island, 19th December, 1938, coll. W. French.

RANGE. Malaupaina and Malaulalo Islands, Three Sisters or Olo Malau group, north of San Cristoval, British Solomon Islands.

DIAGNOSIS. Apparently very like topotypical *santoensis* Mayr (1931*a*) from Espiritu Santo, New Hebrides, but with wider bill. Bill width in mm, taken with vernier calipers at front edges of nostrils:

sororum 4 ♂ ad 13·4, 13·7, 13·8, 13·8; 3 ♀ ad 13·7, 14·4, 14·4.
santoensis 3 ♂ ad 12·6, 12·7, 12·9; 5 ♀ ad 12·8, 12·9, 13·3, 13·4, 13·4.

MATERIAL. Three Sisters: 11 specimens, BM(NH) reg. nos. 1934.8.15.3, 1938.11.23.41–43, 1940.7.4.15–21. All but one collected by W. French, though some marked as collected by W. H. Barrow. Malaupaina: 4 ♂ ad (19th December, 1938, 25–27th March, 1939), 1 ♂ imm (11th May, 1934, coll. R. A. Lever), 1 ♀ ad (19th December, 1938), 1 ♀ imm (25th March, 1934), 1 ? ad (27th February, 1934), 1 ? imm (1st March, 1934). Malaulalo: 2 ♀ ad (30th March, 1939).

Wing 4 ♂ ad 96·5–101 (98·2); 1 ♂ imm 94; 3 ♀ ad 95–100 (98·0); 1 ♀ imm 95; 1 ? ad 99·5; 1 ? imm 95·5. *Tail* 4 ♂ ad 66·5–67·5 (66·9); 3 ♀ ad 63·5–69·5 (67·5); 1 ? ad 68·5. *Bill* (from front of nostril) 4 ♂ ad 38–39 (38·4); 1 ♂ imm 39; 3 ♀ ad 39–42 (40·3); 1 ♀ imm 40; 1 ? ad 37; 1 ? imm 39·5.

Iris " dark brown ". *Bill* " black " (and " white "). *Foot* " dark flesh ", " grey " or " black " (February to May), " dirty white " (December—somewhat paler in dried skins).

DESCRIPTION. Differs from *solomonis*, and agrees with the Southern Melanesian forms (see Mayr, 1931*a*), in having the ringband fully-developed across the nape.

The series is in more or less worn plumage, so that critical comparisons of the blue and ochraceous colours are impossible. However, where comparative material is suitable, reasonable predictions can be made about the coarser differences, and these are given in square brackets. The series has been compared with specimens of *solomonis*, all the Southern Melanesian races, and three from western Polynesia. Compared with :

solomonis (Solomons—San Cristoval and Ugi) : ringband continuous [♂ ringband deeper rufous relative to underparts ; ♂ underparts much less rufous than on San Cristoval ; wing and tail paler and greener relative to mantle].

amoena (Rennell) : much larger [♂ much paler and greener above].

vicina (Sta. Cruz group—Duff group) : bill longer and much wider.

brachyura (Sta. Cruz group—Reef group) : somewhat larger, bill considerably so [♂ ringband relatively deeper rufous, ♀ whiter below].

ornata (Sta. Cruz group—Santa Cruz) : [♂ mainly white below].

utupuae (Sta. Cruz group—Utupua) : supraloral spots much smaller, ringband narrower [♀ paler above].

melanodera (Sta. Cruz group—Vanikoro) : ringband much wider, black nuchal band narrower [less black fringing on breast, mantle much less blackish].

torresiana (New Hebrides—Torres group) : ringband wider, especially above auriculars [♂ mantle duller and greener, ♀ head bluer relative to mantle].

cf. *santoensis* (New Hebrides—Banks group) : ringband wider, especially above auriculars, bill longer and somewhat wider.

santoensis (New Hebrides—Santo) : bill wider [tail relatively paler and greener, head relatively bluer, ♂ under wing-coverts deeper buff].

juliae (New Hebrides—Efate) : bill longer and much wider.

erromangae (New Hebrides—Erromanga) : bill longer and much wider, collar narrower [♂ mainly white below, ♀ underwing almost pure white].

tannensis (New Hebrides—Tanna) : bill longer and much wider, collar narrower [♂ mainly white below, ♀ underwing almost pure white].

cf. *juliae* (New Hebrides—Aneiteum) : bill much wider.

eximia (Fiji—Kandavu) : bill longer and wider, ringband less mixed with blue posteriorly [♂ whiter below].

vitiensis (Fiji—Viti Levu, Ovalau) : bill longer and much wider, ringband wider, especially over auriculars, and less mixed with blue [♂ much whiter below].

sacra (Tonga) : bill longer and wider [♂ underwing with some ochraceous].

NOTES. The general resemblance between *sororum* and *solomonis*, with the one trenchant difference bridged by the ringbanded individual from Goge mentioned above, confirms that the major cleavage between the races characteristic of Southern and of Northern Melanesia lies (despite Mayr, 1931*a* : 10) not between *amoena* and *solomonis*, but between *solomonis* and *alberti*. This affects the faunal affinities of Rennell (see Mayr, 1931*c* ; Bradley & Wolff, 1956 ; Braestrup, 1956). It is remarkable that otherwise similar individuals on Ugi, fourteen miles away, differ so markedly from the Three Sisters population in lacking the ringband altogether.

This subspecies is named in honour of our daughters Angela, Nino and Janet.

(M. 76) ***Halcyon saurophaga saurophaga*** Gould, 1843

REFERENCES. *Cat. Birds. B.M.* 17 : 249. See Mayr, 1949*a* : 56.

RANGE. Moluccas, northern New Guinea and nearby islands, Northern Melanesia except Admiralty and Ninigo groups (coasts).

SPECIMENS. Ugi 3 ♂ ad, 1 ♂ subad ?. 1 ♂ ad to OUM.

Weight 3 ♂ ad 123–146 (132·2) ; 1 ♂ subad 111·5. *Wing* 3 ♂ ad 122–131 (127·8) ; 1 ♂ subad 124. *Tail* 3 ♂ ad 80–84·5 (82·2) ; 1 ♂ subad 80. *Bill* (from nostril) 3 ♂ ad 53–53·5 (53·3) ; 1 ♂ subad 48.

Iris very dark brown. *Bill* black, base of mandible white to very pale grey, pinkish towards extreme base. *Foot* slate-grey, scutes fuscous black.

The " subadult " specimen is here separated solely on measurements, especially bill-length.

(M. 77) ***Halcyon australasia sancta*** Vigors & Horsfield, 1827

REFERENCES. *Cat. Birds B.M.* 17 : 267 ; Keast, 1957 : 68.

RANGE. Southern Australia ; partial migrant, many individuals wintering from Lesser Sunda Isles to Solomons, where a few apparently remain all year (lowlands).

SPECIMENS. Guadalcanal : Tenaru 6 ♂ ad, 2 ♀ ad, 1 ? ad. 1 ♂ ad to OUM.

Weight 6 ♂ ad 46–58 (50·0) ; 2 ♀ ad 54·5, 54·5. *Wing* 6 ♂ ad 88–94·5 (92·0) ; 2 ♀ ad 90, 90. *Tail* 6 ♂ ad 57–61 (58·8) ; 2 ♀ ad 56, 61. *Bill* (from nostril) 6 ♂ ad 32–38 (34·5) ; 2 ♀ ad 32·5, 37·5.

Iris dark to very dark brown. *Bill* black, base of mandible dirty white to silvery, sometimes pinkish. *Foot* fuscous grey, toes blackish.

NOTES. We follow Mayr (1944*b* : 119) and van Bemmel (1948 : 359) in regarding *sancta* as conspecific with *H. australasia* of the Lesser Sunda Isles, despite the overlap in that area outside the breeding-season. In the Solomons, some of the individuals which remain during the breeding season do appear to breed (Cain & Galbraith, 1956 : 263 ; French, 1957). French (*in litt.*) writes of the Three Sisters : " The Sacred Kingfisher (*Halcyon sancta*) bred, and its breeding habits and choice of sites were similar to the White-collared Kingfisher (*Halcyon chloris* [sororum]). Both utilize termites nests on trees in fairly open forest and frequently those on coconut trees in the plantations, and seem to prefer those at a height of from 3 ft. to 10 ft. above ground level. The drilled hole is very like that of our Green Woodpecker [*Picus viridis*] but not nearly so deep. The Beach or White-headed Kingfisher (*Halcyon saurophaga*) always nested in dead and rotting stumps along the shore, and the hole was invariably drilled straight in, and in many cases straight through leaving a double entrance. All three species laid 2 or 3 eggs, the latter being the commonest full clutch."

(M. 78) ***Halcyon leucopygia*** (Verreaux, 1858)

REFERENCES. *Cat. Birds B.M.* 17 : 252 ; Hartert, 1926*b* : 134.

RANGE. Bougainville, Shortland, Choiseul, Ysabel, Florida Is., Guadalcanal (lowlands).

SPECIMENS. Guadalcanal : Tenaru 5 ♂ ad, 6 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 5 ♂ ad 42·5–52 (46·7) ; 6 ♀ ad 43·5–51·5 (49·1). *Wing* 5 ♂ ad 84–92 (87·9) ;

6 ♀ ad 87–90 (88·3). *Tail* 5 ♂ ad 55–63 (56·1) ; 6 ♀ ad 57–61 (58·5). *Bill* (from nostril) 5 ♂ ad 32·5–34·5 (33·7) ; 6 ♀ ad 32·5–34·5 (33·0).

Iris dark brown. *Skin* round eye white. *Bill* black, extreme base of mandible dirty white to blackish. *Foot* dark grey, toes and scutes black, upper shanks purplish.

(M. 79) ***Halcyon bougainvillei excelsa*** Mayr, 1941

References. Mayr, 1941*d* : 3.

Range. Guadalcanal.

Specimens. Guadalcanal : Betilonga 2 ♀ ad. 1 ♀ ad to OUM.

Weight 2 ♀ ad 160, 215. *Wing* 2 ♀ ad 135, 137. *Tail* 2 ♀ ad 99, 100·5. *Bill* (from nostril) 2 ♀ ad 40·5, 41.

Iris dark brown. *Bill* orange. *Foot* orange.

These specimens, whose ovaries were somewhat developed, agree with the hitherto unique holotype in having softer plumage than *H. b. bougainvillei*, so that this does appear to be a racial character (cf. Mayr, 1941*d*). Differences of these two from the holotype (apparently larger ; colours of crown, wing and tail and sizes of collar and rump-patch as in *bougainvillei*) may reflect the fact that the latter is in very worn plumage (P. Vaurie, *in litt.*).

Notes. This race differs from *bougainvillei* chiefly in the pure olive upper back and paler underparts of the female, while the male remains unknown. Despite Mayr (1941*d*), the differences are not very marked, considering the separation of the races and the peculiarity of the species.

(M. 80) *Merops ornatus* Latham, 1801

References. *Cat. Birds B.M.* 17 : 74.

Range. Australia ; migrant, wintering from Celebes to Northern Melanesia.

Notes. The only published records for the Solomons seem to be those of Ramsay (1882*c* : 20).

(M. 81) ***Eurystomus orientalis solomonensis*** Sharpe, 1890

References. Ripley, 1942 : 174.

Range. Feni, Solomons.

Specimens. Guadalcanal ; Betilonga 1 ♂ ad, 3 ♀ ad. San Cristoval : Goge 2 ♂ ad, 1 ♂ juv ; Nagasi 1 ♂ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 4 ♂ ad 149·5–166 (159·0) ; 1 ♂ juv 120 ; 3 ♀ ad 151·5–185 (166·8). *Wing* 4 ♂ ad 190·5–201 (197·8) ; 3 ♀ ad 191–200·5 (197·0). *Tail* 4 ♂ ad 125–134 (129·9) ; 2 ♀ ad 132, 136. *Bill* (from feathering) 4 ♂ ad 23–23·5 (23·2) ; 1 ♂ juv 14 ; 3 ♀ ad 21·5–24 (22·5).

Iris dark brown. *Eyelid* dull orange. *Bill* orange-red, sometimes pinkish ; juv maxilla black with flesh-coloured base and edges, mandible flesh-colour. *Foot* dull orange-red, claws blackish ; juv pinkish fawn, washed with fuscous on toes, purplish on shanks.

(M. 82) ***Rhyticeros plicatus mendanae*** Hartert, 1924

REFERENCES. Mayr, 1934*a* : 10 ; Sanft, 1960 : 120.

RANGE. Choiseul, Ysabel, Guadalcanal, Malaita.

SPECIMENS. Guadalcanal : Betilonga 1 ♂ ad, 1 ♀ ad. To OUM.

Wing 1 ♀ ad 386. *Tail* 1 ♀ ad 227. *Bill* 1 ♂ ad 185·5 ; 1 ♀ ad 169.

Iris ♂ orange, ♀ brown. *Skin* round eye blue ; eyelid ♂ red, ♀ grey ; throat white. *Bill* dark red basally, tip pale horn. *Foot* black.

(M. 84) *Hirundo tahitica subfusca* Gould, 1856

REFERENCES. Mayr, 1934*a* : 13 ; 1955 : 6.

RANGE. Polynesia to Solomons and Lihir, intergrading via New Ireland with *H. t. ambiens* (coasts).

(M. 85) *Hirundo nigricans nigricans* Vieillot, 1817

REFERENCES. White, 1936 : 90.

RANGE. Australia ; migrant, wintering in New Guinea region and Northern Melanesia (mainly lowlands).

NOTES. Only two specimens have been recorded from the Solomons, both from Guadalcanal (Hartert, 1929 : 7 ; Mayr, 1955 : 6).

(M. 86) ***Lalage leucopyga affinis*** (Tristram, 1879)

REFERENCES. Mayr & Ripley, 1941 : 17.

RANGE. San Cristoval, Ugi.

SPECIMENS. San Cristoval : Manewiriwiri 1 ♂ ad ; Goge 1 ♂ ad, 2 ♂ imm, 3 ♀ ad, 2 ♀ imm, 2 ? juv ; Nagasi 1 ♂ ad, 2 ♀ ad. Ugi 8 ♂ ad, 1 ♂ imm, 4 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight San Cristoval 3 ♂ ad 24–25 (24·2) ; 2 ♂ imm 21, 24·5 ; 5 ♀ ad 21–28 (24·3) ; 1 ♀ imm 24 ; Ugi 8 ♂ ad 23·5–27 (25·6) ; 1 ♂ imm 23·5 ; 4 ♀ ad 24–26 (24·9). *Wing* San Cristoval 3 ♂ ad 81·5–87 (84·2) ; 2 ♂ imm 80, 82·5 ; 4 ♀ ad 80–82·5 (81·6) ; 2 ♀ imm 79, 84 ; Ugi 8 ♂ ad 82·5–87·5 (85·1) ; 1 ♂ imm 78·5 ; 4 ♀ ad 80–85 (82·9). *Tail* San Cristoval 1 ♂ ad 74 ; 1 ♂ imm 68 ; 1 ♀ ad 75 ; 2 ♀ imm 66, 74 ; Ugi 6 ♂ ad 66–76 (71·5) ; 2 ♀ ad 69·5, 73. *Bill* San Cristoval 3 ♂ ad 17·5–18 (17·7) ; 2 ♂ imm 17, 17·5 ; 3 ♀ ad 17·5–18 (17·7) ; 2 ♀ imm 17·5, 18 ; Ugi 7 ♂ ad 16–18 (17·3) ; 1 ♂ imm 18 ; 3 ♀ ad 17·5–18·5 (18·0).

Iris very dark brown *Bill* black, base of mandible paler—♂ more or less grey, ♀ grey to horn ; imm pale area yellower and more extensive ; juv gape yellow. *Foot* dark grey or black, upper shank fuscous or brownish.

One of the immature males from Goge had enlarged testes.

NOTES. Clearly the single very large male from Ugi (Mayr & Ripley, 1941) was not characteristic of the population.

(M. 87) ***Coracina holopolia holopolia*** (Sharpe, 1888)

REFERENCES. Sharpe, 1888 : 184 ; Rothschild & Hartert, 1901*c* : 374 ; Mayr, 1931*f* : 17.

RANGE. Buka, Bougainville, Choiseul, Ysabel, Guadalcanal (mainly lowlands ?).

SPECIMENS. Guadalcanal: Tenaru 1 ♀ imm; Betilonga 1 ♀ subad.

Weight 1 ♂ ad 43; 1 ♀ subad 41; 1 ♀ imm 47. *Wing* 1 ♀ subad 105; 1 ♀ imm 104. *Bill* 1 ♀ subad 25; 1 ♀ imm 23·5.

Iris dark brown. *Bill* black; subad and imm fuscous to dark grey. *Foot* black.

Neither the juvenile nor the immature plumages have been described for this species, and the latter is not represented in the AMNH (P. Vaurie, *in litt.*), while geographical variation has been studied only in the adult male. The subadult is in adult plumage, except for its juvenile remiges (as retained by immatures), apparently immature axillaries and under wing-coverts, and a single immature feather on the lower breast. The immature is moulting from the juvenile to the immature plumage, but accidental loss and replacement of some feathers has superficially confused its plumage sequence: some of the secondaries in the right wing are essentially adult, while an underlying patch of feathers on the right lower breast is more worn and more juvenile in character (more boldly barred, the white tinged with yellow) than the surrounding immature plumage. The immature contour-feathers are grey above as in the adult, but on throat, breast, under tail-coverts, under wing-coverts and axillaries they are boldly barred in black and white, grading on the flanks and belly into grey with narrow white bars.

The juvenile plumage, softer than the succeeding ones, is fuscous and fawn in colour. The rectrices are pointed, the central pair grey and the remainder browner than in the adult, with a terminal pattern best developed on the outermost feathers. This pattern consists of a wide fawn tip, not extending far up the margins of the webs, which bears a dark line parallel to the margin on each side, and indications of a second line within this. The wing feathers are fuscous, with fawn outer margins expanding into wider tips. The tips of the coverts and inner secondaries bear a pattern of two dark bars similar to that on the tail. Both bars run straight across the tip, while the inner one bends sharply at each end to run for a short distance parallel to the edges of the feather; the inner edge of this bar is ill-defined. The contour feathers are square-cut, fawn with brown cross bars. On head and back there are two straight bars, while on breast and flanks there is usually a single }-shaped bar, and a vague shaft-streak basally.

NOTES. The juvenile plumage is very different from that of *Coracina lineata*, in which the pale areas are yellowish white and the dark blackish, the contour feathers rounded, with pale edges (giving a scalloped effect) on the underparts, and the pale edges on remiges and rectrices simple. The immature plumage, with its ventral barring and white-flecked auriculars, is reminiscent of the female of *C. dohertyi* (which represents the *morio-tenuirostris* superspecies on Sumba and Flores—Stresemann, 1939: 124; Mayr, 1944*a*: 142), though its barring is less bold.

An adult male, too damaged to be retained, was taken near Tsea. The locality Tenaru was omitted by Cain & Galbraith (1956: 266). Thus two of the three specimens were taken in the lowlands. The vertical distribution of the species is not clear: possibly it is subject to geographical variation.

This species and the *morio-tenuirostris* superspecies were formerly placed in *Edolisoma*, now considered as merely a subgenus of *Coracina* (Delacour, 1946: 2; see Mayr, 1955).

(M. 88) ***Coracina tenuirostris erythropygia*** (Sharpe, 1888)

REFERENCES. Rothschild & Hartert, 1901*c* : 373 ; 1902 : 582 ; Mayr, 1931*f* : 18 ; 1955 : 12.

RANGE. Guadalcanal and Malaita Groups, with slight geographical variation.

SPECIMENS. Guadalcanal : Tenaru 2 ♂ ad ; 2 ? imm ; Betilonga 11 ♂ ad, 4 ♀ ad, 1 ♀ imm, 3 ? imm, 1 ? juv ; Turipava 1 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 11 ♂ ad 54–63 (58·1) ; 2 ♂ imm 54, 61·5 ; 5 ♀ ad 52–64·5 (57·4) ; 1 ♀ imm 55. *Wing* 10 ♂ ad 113–120 (117·5) ; 1 ♂ imm 112 ; 5 ♀ ad 109–113·5 (111·5) ; 1 ♀ imm 112. *Bill* 9 ♂ ad 25·5–29 (27·0) ; 2 ♂ imm 26·5, 26·5 ; 4 ♀ ad 26–27·5 (26·6) ; 1 ♀ imm 26.

Iris dark brown. *Bill* black, base of ♀ mandible sometimes paler ; imm maxilla fuscous to blackish, mandible pale horn to warm grey with darker tip ; juv bill dull brown. *Foot* fuscous black, ♀ sometimes paler ; imm and juv dark grey.

Apart from their juvenile remiges and rectrices, the immatures differ from adult females in having the cap brown instead of grey and the mantle more rufous, less greyish or olivaceous.

In the juvenile plumage, each upper wing-covert and inner secondary has a rufous tip bearing a white terminal spot and a blackish bar. The head is yet more brown than that of immatures, with whitish fringes. The underparts bear dark drop-shaped shaft-streaks.

One of the adult females (BM(NH) reg. no. 1959.21.542) has sparse and irregular shaft-streaking and barring of the underparts. This seems relevant to the origin of the barred race *nisoria* of the Russell Is. (see Mayr, 1955 : 13).

(M. 88) ***Coracina salomonis*** (Tristram, 1879)

REFERENCES. Ramsay, 1883 : 667 ; Rothschild & Hartert, 1908*b* : 362 ; Mayr, 1955 : 12.

RANGE. San Cristoval.

SPECIMENS. San Cristoval : Goge 13 ♂ ad, 3 ♂ imm, 8 ♀ ad, 1 ♀ imm, 1 ? imm ; Nagasi 3 ♂ ad, 2 ♂ imm, 6 ♀ ad, 1 ♀ imm, 2 ? juv. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 15 ♂ ad 55–75 (64·6) ; 5 ♂ imm 62·5–65·5 (63·8) ; 12 ♀ ad 60·5–73 (65·7) ; 1 ♀ imm 64·5. *Wing* 14 ♂ ad 117–122·5 (119·2) ; 5 ♂ imm 115·5–118 (116·5) ; 12 ♀ ad 115–120·5 (117·4) ; 2 ♀ imm 112, 112. *Bill* 15 ♂ ad 27·5–32 (28·9) ; 4 ♂ imm 27·5–29·5 (28·4) ; 14 ♀ ad 28–30·5 (29·4) ; 2 ♀ imm 28·5, 29.

Iris very dark brown ; juv dark grey-brown. *Bill* black ; imm gape and base of mandible sometimes grey ; juv mandible grey or brown with pale subterminal spot. *Foot* black, shanks sometimes brownish ; juv dark grey.

The immatures are indistinguishable from adult females, except for their juvenile wings and tails. In the juvenile plumage, the wing-feathers have the white terminal spots obsolete and the dark subterminal bars not clearly demarcated. The feathers of the crown are dark fuscous grey, with black subterminal bars and whitish-buff tips ; those of the mantle and the upper tail-coverts have white tips, followed by rufous and then by black subterminal bars. The underparts are paler than those of immatures and adult females, with vague blackish streaks-shaft and whitish tips.

NOTES. In *Coracina*, two character-series can be traced in the female plumage, in each of which the first-mentioned term is closest to the male and the last to the juvenile plumage. The series in distribution of eumelanins runs : all-grey—grey with narrow pale bars—black, grey and pale bars—pale with narrow black bars—all-pale. That in the intensity of phaeomelanins in the pale areas runs : none (white)—pale (buff)—deep (rufous). Total cock-feathering has clearly arisen repeatedly in the *morio-tenuirostris* superspecies. However, discordance between the coloration of dorsal and ventral surfaces is rare, being confined to the females of *morio* and closely-related races in Celebes, *dohertyi* of Flores and Sumba, and *salomonis*. In the two former, the underparts lie towards the " male " ends of both character series, whereas in *salomonis* they are as " juvenile " as possible. In all three, the upperparts are as in the adult male. Since *morio* is sympatric with a characteristic form (*edithae*) of *C. tenuirostris*, while Mayr (1944*a* : 142) considers *dohertyi* as a full species, and since *salomonis* is also distinct in the more conservative male plumage, it should be considered as another representative species.

(M. 89) **Coracina lineata solomonensis** (Ramsay, 1879)

REFERENCES. Ramsay, 1879*a* : 71 ; Tristram, 1892 : 294 ; Rothschild & Hartert, 1905 : 264 (*pusillus*) ; Mayr, 1931*f* : 17 ; 1955 : 14. See Ripley, 1941 ; Voous & van Marle, 1949.

RANGE. Guadalcanal.

SPECIMENS. Guadalcanal : Tenaru 1 ♂ ad ; Tasinasa 1 ♀ ad ; Betilonga 5 ♂ ad, 6 ♀ ad ; Turipava 1 ♂ ad, 1 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 7 ♂ ad 56–64 (60·4) ; 8 ♀ ad 50–65·5 (58·9). *Wing* 7 ♂ ad 129–135 (131·8) ; 8 ♀ ad 124·5–129·5 (126·3). *Bill* (from front of nostril) 7 ♂ ad 10·5–12 (11·2) ; 8 ♀ ad 11–11·5 (11·1).

Iris yellow. *Bill* black. *Foot* black.

The males show considerable variation, between individuals and between the feathers of one individual, in the degree of barring of under wing-coverts and axillaries; the extremes being blue-grey with faint white bars on the one hand, and boldly barred in black and white on the other. The barred feathers are probably remnants of the immature plumage, which (in *solomonensis*, *ombriosa*, *nigrifrons*, and *axillaris* at least) is ventrally barred (P. Vaurie, *in litt.*).

(M. 89) **Coracina lineata makirae** Mayr, 1935

REFERENCES. Mayr, 1936 : 13. See Ripley, 1941 ; Voous & van Marle, 1949.

RANGE. San Cristoval.

SPECIMENS. San Cristoval : Goge 8 ♂ ad, 10 ♂ imm, 8 ♀ ad, 2 ♀ imm, 1 ♀ juv, 1 ? imm ; Nagasi 1 ♂ ad, 1 ♂ imm, 1 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM ; 1 ♂ imm to AMNH.

Weight 7 ♂ ad 70–78·5 (73·9) ; 9 ♂ imm 61–75 (71·8) ; 7 ♀ ad 65·5–84·5 (73·5) ; 2 ♀ imm 69·5, 70 ; 1 ♀ juv 66·5. *Wing* 8 ♂ ad 135·5–144 (139·4) ; 10 ♂ imm 130·5–137 (133·4) ; 9 ♀ ad 133–140 (137·3) ; 2 ♀ imm 132, 132 ; 1 ♀ juv 129. *Bill* (from front of nostril) 8 ♂ ad 12·5–14 (13·3) ; 9 ♂ imm 13–14 (13·3) ; 7 ♀ ad 12–13·5 (13·1) ; 2 ♀ imm 12·5, 13 ; 1 ♀ juv 13.

Iris bright lemon-yellow ; imm bright lemon-yellow to pale yellowish grey ; juv pale grey-brown. *Bill* black ; juv gape flesh-coloured. *Foot* black ; juv dark slate.

Immature individuals have juvenile wings and tails, and sometimes dull irides. They are otherwise indistinguishable from adult females, except that the barring is occasionally black-and-white, as in adults of the wholly hen-feathered races *gracilis* and *lineata*, instead of having grey inner halves to the dark bars. Two immature specimens each of *gracilis* (Bradley & Wolff, 1956 : 104, nos. 125 and 131) and *lineata*, and one of *sublineata*, have the white bars markedly wider than in corresponding adult females. Before the immaturity of the heavily-barred males was recognized, *makirae* was erroneously mentioned as an unusually variable race (Galbraith, 1956 : 162).

NOTES. There seems no reason to suppose that *gracilis* of Rennell is more closely related to *lineata* of Australia than to the Melanesian races, despite Mayr (1931*b* : 18 ; 1955 : 14). They are linked by their complete hen-feathering, and by the associated " juvenility " of their barring, without any grey (see p. 50). The races *makirae*, *malaitae* and *sublineata* are intermediate in degree of dimorphism, while some immatures of the former show black-and-white barring. In other respects, the small dark *gracilis* is more similar to the Solomons races than to the large pale *lineata*. In fact, Mayr (1931*c* : 7 ; followed by Bradley & Wolff, 1956 : 115) elsewhere lists *gracilis* as more closely related to the races in the Solomons.

(M. 90) ***Coracina papuensis elegans*** (Ramsay, 1881)

REFERENCES. Rothschild & Hartert, 1916 : 289 ; Mayr, 1931*f* : 16 ; 1955 : 13. See Ripley, 1941 ; Voous & van Marle, 1949.

RANGE. Guadalcanal, Russell Is., New Georgia Group (mainly lowlands).

SPECIMENS. Guadalcanal : Tenaru 9 ♂ ad, 4 ♀ ad, 1 ? imm, 1 ? juv : Betilonga 1 ♂ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 10 ♂ ad 56–64 (61·2) ; 4 ♀ ad 58·5–65 (61·1). *Wing* 9 ♂ ad 130–137 (132·3) ; 4 ♀ ad 127–136 (131·8). *Bill* (from front of nostril) 7 ♂ ad 16–18 (17·4) ; 3 ♀ ad 16–17·5 (17·0).

Iris very dark brown. *Bill* black ; juv maxilla blackish, mandible dark horn with blackish tip, gape yellow. *Foot* grey, scutes black ; juv pale fuscous grey, claws black and dull white, soles very pale yellow.

Apart from its juvenile wing and tail, the immature differs from adults in its duller black mask and whiter breast.

The Betilonga specimen was taken " in native gardens near village ", not in forest, despite Cain & Galbraith (1956 : 267).

(M. 91) ***Coracina caledonica amadonis*** Cain & Galbraith, 1955

REFERENCES. Cain & Galbraith, 1955 : 90. See Mayr, 1955 : 15. See Ripley, 1941 ; Voous & van Marle, 1949.

RANGE. Guadalcanal (mountains).

SPECIMENS. Guadalcanal : Turipava 2 ♂ ad, 1 ♀ ad. 1 ♂ ad to AMNH.

Weight 2 ♂ ad 133·5, 136 ; 1 ♀ ad 165. *Wing* 2 ♂ ad 176, 180 ; 1 ♀ ad 173. *Bill* 2 ♂ ad 35, 36·5 ; 1 ♀ ad 38·5.

Iris dark red-brown. *Bill* black. *Foot* black.

The holotype (adult female, expedition no. 459) is BM(NH) reg. no. 1959.21.434.

NOTES. This is the most distinct race in the species.

(M. 92) *Coracina novaehollandiae melanops* (Latham, 1801)

REFERENCES. *Cat. Birds B.M.* 4 : 30 ; Keast, 1958 : 253. See Ripley, 1941 ; Voous & van Marle, 1949.

RANGE. Southern and eastern Australia ; migrant, wintering in eastern New Guinea region, Bismarcks, and occasionally Solomons (coasts).

NOTES. Recorded from the northern Solomons only, Nissan (Mayr, 1955 : 17) and Bougainville (Baker, 1948 : 17)—both records in August.

(M. 93) ***Turdus poliocephalus sladeni*** Cain & Galbraith, 1955

REFERENCES. Cain & Galbraith, 1955 : 92. See Mayr, 1931*b* : 21 ; 1941*d* : 6.

RANGE. Guadalcanal (mountains).

SPECIMENS. Guadalcanal : Turipava 1 ♂ ad, 2 ♂ subad, 1 ? subad. 1 ♂ subad to AMNH.

Weight 4 ♂ ad & subad 57–67·5 (61·9). *Wing* 4 ♂ ad & subad 107–111·5 (109·6). *Tail* 4 ♂ ad & subad 82–87 (84·5). *Bill* 4 ♂ ad & subad 23–24·5 (23·7).

Iris dark brown. *Eyelid* yellow. *Bill* yellow. *Foot* yellow, shins and claws fuscous-tinged.

The holotype (adult male, expedition no. 544) is BM(NH) reg. no. 1959.21.553.

(M. 95) ***Zoothera margaretae turipavae*** Cain & Galbraith, 1955

REFERENCES. Cain & Galbraith, 1955 : 92. See Mayr, 1955 : 17.

RANGE. Guadalcanal (mountains).

SPECIMENS. Guadalcanal : Turipava 1 ♂ ad.

Weight 53·5. *Wing* 90·5. *Tail* 63·5. *Bill* 24·5.

Iris very dark brown. *Bill* black, base greyish, gape dull orange. *Foot* greyish fuscous, joints paler and greyer, claws ivory.

The unique holotype (expedition no. 485) is BM(NH) reg. no. 1959.21.557.

(M. 95) *Zoothera margaretae margaretae* (Mayr, 1935)

REFERENCES. Mayr, 1936 : 14. See Mayr, 1955 : 17.

RANGE. San Cristoval (mountains).

(G) ***Cichlornis whitneyi turipavae*** Cain & Galbraith, 1955

REFERENCES. Cain & Galbraith, 1955 : 91. See Mayr, 1945*a* : 191 ; Gilliard, 1960*b*.

RANGE. Guadalcanal (mountains).

SPECIMENS. Guadalcanal : Turipava 1 ♂ ad.

Weight 36. *Wing* 65·5.

Iris dark brown. *Bill* blackish, mandible streaked with whitish, gape dull yellow. *Foot* fuscous brown.

The unique holotype (expedition no. 448) is BM(NH) reg. no. 1959.21.558.

NOTES. In the scattered group of babbler-warblers to which *Cichlornis* appears to belong (Mayr, 1933*a* : 3 ; 1944*a* : 158 ; 1955 : 18 ; Cain & Galbraith, 1955 : 91), two subgroups (whether phyletic or adaptive) are discernible. On the one hand there are pale-coloured, relatively long-tailed forms, somewhat resembling *Megalurus*, in open and more or less arid habitats : *Buetikoferella bivittata* of Timor, *Eremiornis carteri* of Australia and *Megalurulus marei* of New Caledonia. On the other, there is an even more scattered subgroup of dark-coloured, shorter-tailed forms, with less depressed nasal opercula, occupying the dense wet forest on mountainous islands : *Cichlornis w. whitneyi* on Santo, *C. w. turipavae* on Guadalcanal, *C. grosvenori* and *Ortygocichla rubiginosa* on New Britain, and *O. rufa* on Viti Levu. With the recent discovery of *Cichlornis grosvenori* Gilliard (1960*b*), the mountains of New Britain become the only locality known to support two species of this group.

(M. 96) ***Vitia parens*** Mayr, 1935

REFERENCES. Mayr, 1936 : 15.

RANGE. San Cristoval (mountains).

SPECIMENS. San Cristoval : Nagasi 1 ♀ ad, 1 ♀ imm.

Weight 1 ♀ ad 14 ; 1 ♀ imm 13. *Wing* 1 ♀ ad 55. *Tail* 1 ♀ imm 42. *Bill* 1 ♀ imm 17·5.

Iris brown ; imm dark grey-brown. *Bill* maxilla black, mandible grey with whitish base, gape pale grey, dull yellow internally ; imm mandible with whitish stripe and yellowish tip, gape dull yellow. *Foot* dull yellow, toes and fronts of shanks washed dark brown.

The immature specimen, whose wings are not fully-grown, has the crown duller and less rufous than the adult, but retains none of the juvenile plumage described by Mayr (1936).

(M. 97) ***Acrocephalus stentoreus cervinus*** de Vis, 1897

REFERENCES. Mayr, 1948 : 209 ; 1955 : 18.

RANGE. Sumba, northern Queensland, scattered localities in New Guinea, New Britain, Solomons—Bougainville, Gijunabena near Ysabel, Guadalcanal (lowlands).

SPECIMENS. Guadalcanal : Tenaru 3 ♂ ad, 1 ♀ ad.

Weight 3 ♂ ad 17·5–18 (17·8) ; 1 ♀ ad 16. *Wing* 3 ♂ ad 68·5–71·5 (69·8) ; 1 ♀ ad 65·5. *Tail* 3 ♂ ad 63–64·5 (63·5) ; 1 ♀ ad 62. *Bill* 3 ♂ ad 20–22 (21·2) ; 1 ♀ ad 20·5.

Iris yellowish brown. *Bill* maxilla blackish with yellowish horn edges, mandible yellowish horn with greyer tip, gape flesh-colour. *Foot* brownish grey, shanks browner.

(M. 99) ***Phylloscopus trivirgatus becki*** Hartert, 1929

REFERENCES. Hartert, 1929 : 13 ; Mayr, 1936 : 17.

RANGE. Ysabel, Guadalcanal, Malaita (mountains).

SPECIMENS. Guadalcanal : Turipava 2 ♂ ad.

Weight 2 ♂ ad 10, 11·5. *Wing* 1 ♂ ad 59. *Tail* 1 ♂ ad 44·5. *Bill* 1 ♂ ad 14.

Iris dark brown. *Bill* maxilla blackish, mandible horn, paler basally. *Foot* pale blue-grey, tinged with fuscous, sole dull yellow.

Notes. The remark (Mayr, 1955 : 19) that the species is to be expected from Guadalcanal is of course a lapse, since this was one of the first birds to be discovered in the mist-forest of Guadalcanal.

(M. 99) ***Phylloscopus trivirgatus makirensis*** Mayr, 1935

References. Mayr, 1936 : 18.

Range. San Cristoval (mountains).

Specimens. San Cristoval : Nagasi 2 ♂ ad, 2 ♀ ad.

Weight 2 ♂ ad 9, 9·5 ; 2 ♀ ad 9, 9·5. *Wing* 2 ♂ ad 50·5, 53 ; 2 ♀ ad 48·5, 49. *Tail* 2 ♂ ad 37·5, 39·5 ; 1 ♀ ad 35. *Bill* 1 ♂ ad 13·5 ; 2 ♀ ad 13, 13·5.

Iris dark brown. *Bill* maxilla black (♀ with yellowish edge), mandible greyish or greenish horn with dark brown subterminal patch, gape dull yellow to pale fuscous with yellow tinge. *Foot* bluish grey, ♂ shank blotched with blackish.

(M. 100) ***Rhipidura rufifrons rufofronta*** Ramsay, 1879

References. Mayr, 1931*e* : 19. See Mayr & Moynihan, 1946.

Range. Guadalcanal.

Specimens. Guadalcanal : Tsea 1 ♂ ad ; Betilonga 7 ♂ ad, 3 ♀ ad, 2 ? ad. 1 ♂ ad to OUM.

Weight 8 ♂ ad 11–12 (11·6) ; 4 ♀ ad 10·5–14·5 (11·9). *Wing* 8 ♂ ad 70–74·5 (72·7) ; 3 ♀ ad 68–72 (69·3). *Tail* 5 ♂ ad 80·5–84 (82·4) ; 2 ♀ ad 80·5, 84·5. *Bill* 8 ♂ ad 13·5–15·5 (14·3) ; 2 ♀ ad 14, 14·5.

Iris dark brown. *Bill* black, base of mandible whitish to pale grey or horn. *Foot* grey, brownish to bluish.

(M. 100) ***Rhipidura rufifrons russata*** Tristram, 1879

References. Mayr, 1931*e* : 18. See Mayr & Moynihan, 1946.

Range. San Cristoval.

Specimens. San Cristoval : Manewiriwiri 1 ♂ ad, 1 ♂ imm, 1 ? imm ; Goge 9 ♂ ad, 10 ♂ imm, 7 ♀ ad, 2 ♀ imm, 3 ? imm ; Nagasi 2 ♂ ad, 1 ♂ imm, 1 ♀ ad, 1 ? imm. 1 ♂ ad to OUM.

Weight 13 ♂ ad 8·5–10 (9·1) ; 13 ♂ imm 8·5–10 (9·2) ; 9 ♀ ad 8–9·5 (8·5) ; 2 ♀ imm 8, 8·5. *Wing* 11 ♂ ad 63–68 (65·2) ; 11 ♂ imm 61–68 (63·0) ; 8 ♀ ad 60·5–65·5 (62·4) ; 2 ♀ imm 61, 61. *Tail* 6 ♂ ad 71·5–75 (73·3) ; 6 ♂ imm 67–74 (70·7) ; 3 ♀ ad 70·5–73 (71·8) ; 1 ♀ imm 71·5. *Bill* 11 ♂ ad 12·5–14·5 (13·5) ; 11 ♂ imm 12·5–14 (13·5) ; 8 ♀ ad 13–14 (13·3) ; 2 ♀ imm 13·5, 14.

Iris very dark brown. *Bill* black, base of mandible ivory, sometimes horn-coloured or pinkish ; imm mandible occasionally purplish with orange gape and base, only tip blackish. *Foot* dark grey, usually somewhat fuscous, browner towards upper shank.

In this worn and badly-prepared series, the immature birds are separated only by the rufous edges of their wing-feathers, since their gorgets do not seem to be uniformly duller nor their plumage softer. The development of the gonads tends to support this separation, since there is little overlap between the adult and immature series : but see under *ugiensis* below.

(M. 100) ***Rhipidura rufifrons ugiensis*** Mayr, 1931

REFERENCES. Mayr, 1931*e* : 19. See Mayr & Moynihan, 1946.

RANGE. Ugi.

SPECIMENS. Ugi 3 ♂ ad, 4 ♂ imm, 4 ♀ ad, 2 ♀ imm. 1 ♀ ad to OUM.

Weight 3 ♂ ad 10·5–11·5 (11·0) ; 4 ♂ imm 10·5–12 (10·9) ; 4 ♀ ad 10–10·5 (10·4) ; 2 ♀ imm 10·5, 10·5. *Wing* 1 ♂ ad 71 ; 3 ♂ imm 64–74 (68·3) ; 3 ♀ ad 65–67 (66·0) ; 2 ♀ imm 62, 64. *Tail* 1 ♂ ad 72·5 ; 3 ♂ imm 76–80 (77·7) ; 3 ♀ ad 72–75 (73·5) ; 2 ♀ imm 73·5, 74·5. *Bill* 2 ♂ ad 14·5, 14·5 ; 4 ♂ imm 14–15 (14·2) ; 4 ♀ ad 13·5–14·5 (14·0) ; 2 ♀ imm 13·5, 14.

Iris very dark brown. *Bill* black, base of mandible ivory, sometimes grey or horn-coloured. *Foot* dark grey, somewhat fuscous, brownish towards upper shank.

In this series, shorter and worse-preserved than that of *russata*, the separation of immatures from adults is more dubious : there is more overlap in gonadial development, and the distributions of rufous edges to the wings, duller black throats, and whitish chins (the two last mentioned as characteristic of juveniles in another black-throated race, *melanolaema*, by Mayr, 1931*e*) do not coincide.

(M. 100) *Rhipidura rufifrons kuperi* Mayr, 1931

REFERENCES. Mayr, 1931*e* : 18. See Mayr & Moynihan, 1946.

RANGE. Santa Ana, Santa Catalina.

(M. 101) ***Rhipidura drownei ocularis*** Mayr, 1931

REFERENCES. Mayr, 1931*e* : 12.

RANGE. Guadalcanal (mountains).

SPECIMENS. Guadalcanal : Turipava 4 ♂ ad, 1 ♂ juv, 3 ♀ ad, 2 ? ad. 1 ? ad to OUM.

Weight 4 ♂ ad 11·5–12·5 (12·0) ; 3 ♀ ad 10–10·5 (10·3). *Wing* 4 ♂ ad 72·5–77·5 (75·1) ; 1 ♂ juv 72 ; 3 ♀ ad 68·5–70 (69·2). *Tail* 3 ♂ ad 81–82·5 (81·5) ; 1 ♂ juv 72 ; 2 ♀ ad 73, 75. *Bill* 4 ♂ ad 14–15 (14·2) ; 1 ♂ juv 15 ; 3 ♀ ad 13–13·5 (13·3).

Iris dark brown, sometimes greyish. *Bill* maxilla black, mandible white (sometimes tinged with pink or mauve), tip blackish. *Foot* dark fuscous or brownish grey, sole pale yellow.

(M. 102) ***Rhipidura tenebrosa*** Ramsay, 1881

REFERENCES. Mayr, 1931*e* : 12.

RANGE. San Cristoval.

SPECIMENS. San Cristoval : Goge 3 ♂ ad, 2 ♀ ad, 4 ? ad ; Nagasi 2 ♂ ad, 2 ♀ ad. 1 ? ad to OUM.

Weight 5 ♂ ad 18·5–19·5 (18·9) ; 4 ♀ ad 15·5–16·5 (15·9). *Wing* 4 ♂ ad 84–90 (85·9) ; 4 ♀ ad 75–79·5 (77·7). *Tail* 4 ♂ ad 88–95·5 (92·1) ; 2 ♀ ad 86, 86·5. *Bill* 4 ♂ ad 16–18 (17·0) ; 4 ♀ ad 16.

Iris dark or very dark brown. *Bill* maxilla black, mandible mainly whitish or pale grey (sometimes mauve-tinged) with blackish tip and edges of variable extent. *Foot* fuscous grey with bluish grey patches.

(M. 103) *Rhipidura fuliginosa* cf. *brenchleyi* Sharpe, 1879

References. Mayr, 1931*e* : 14.

Range. San Cristoval (mountains).

Notes. It is unfortunate that this is one of the high-altitude species missed by the expedition on San Cristoval, since the only known series is too worn to show the expected differences from *brenchleyi* of the New Hebrides (Mayr, 1931).

Reversion by Mayr (1955 : 20) to the name *R. flabellifera* (Gmelin, 1789) instead of *R. fuliginosa* (Sparrman, 1787), is clearly a lapse.

(M. 105) ***Rhipidura cockerelli cockerelli*** (Ramsay, 1879)

References. Mayr, 1931*e* : 4.

Range. Guadalcanal.

Specimens. Guadalcanal : Betilonga 8 ♂ ad, 3 ♂ imm, 4 ♀ ad, 1 ♀ imm, 2 ? ad. 1 ♂ ad to OUM.

Weight 8 ♂ ad 16·5–18·5 (17·6) ; 3 ♂ imm 15–16·5 (15·7) ; 4 ♀ ad 17–18 (17·4) ; 1 ♀ imm 15. *Wing* 8 ♂ ad 87–93 (90·1) ; 3 ♂ imm 84–86 (84·8) ; 4 ♀ ad 81–86·5 (83·5) ; 1 ♀ imm 78·5. *Tail* 7 ♂ ad 80–85 (82·7) ; 3 ♂ imm 81–84 (82·0) ; 4 ♀ ad 79–82·5 (80·5) ; 1 ♀ imm 75·5. *Bill* 8 ♂ ad 18–20·5 (19·0) ; 3 ♂ imm 18·5–20 (19·2) ; 3 ♀ ad 18·5–20 (19·5) ; 1 ♀ imm 18.

Iris dark brown. *Bill* black. *Foot* black, occasionally dark fuscous or grey.

Notes. Though the fact has apparently never been remarked (except by Galbraith 1956 : 193), this species is clearly the geographical representative of the widespread and highly polytypic *R. rufiventris*. This makes it less surprising (Mayr, 1955 : 21) that the latter is absent from the Solomons. *R. rufiventris* shows tendencies (especially in *kordensis* of Biak) towards melanism, white spotting of the breast, and loss of all phaeomelanin, which are carried to extremes in *R. cockerelli*. Though much the largest form in the superspecies, *R. cockerelli coultasi* of Malaita approaches certain races of *R. rufiventris* in its white throat, reduced white wing-patch, and grey back. In behaviour, *R. cockerelli* is very unlike the smaller species of *Rhipidura* (Cain & Galbraith, 1956 : 271), though this is not apparent from other accounts (Mayr, 1945*a* ; Virtue, 1947 ; Sibley, 1951) ; while *R. rufiventris* apparently approaches the same *Myiagra*-like mode of feeding (Mayr & Rand, 1937 : 159 ; Mayr & Schauensee, 1939 : 32). In Malaysia, the *rufiventris* superspecies seems to be represented by a doublet : *R. perlata* and *R. euryura*.

(M. 106) ***Rhipidura leucophrys melaleuca*** (Quoy & Gaimard, 1830)

References. Mayr, 1931*e* : 2.

Range. Moluccas, New Guinea region, Northern Melanesia.

Specimens. Guadalcanal : Tenaru 2 ♂ ad, 1 ♀ ad, 1 ♀ imm ; Betilonga 2 ♂ ad, 1 ♀ ad ; Nala 1 ♂ ad. San Cristoval : Manewiriwiri 1 ♀ imm ; Goge 1 ♂ ad, 1 ♂ imm, 1 ♀ ad. Ugi 1 ♂ ad, 3 ♂ imm, 2 ♀ ad, 1 ♀ imm. 1 ♂ ad to OUM.

Weight 7 ♂ ad 31·5–37 (34·4) ; 4 ♂ imm 30–34 (32·4) ; 5 ♀ ad 27–36 (31·7) ; 3 ♀ imm 29–30 (29·3). *Wing* 7 ♂ ad 96–102 (99·2) ; 4 ♂ imm 97–100 (98·6) ; 5 ♀ ad 96–102 (98·5) ; 2 ♀ imm 95·5, 99. *Tail* 6 ♂ ad 93–101 (97·4) ; 2 ♂ imm 94, 95·5 ;

4 ♀ ad 95–100·5 (97·7) ; 3 ♀ imm 91·5–98·5 (94·3). *Bill* 6 ♂ ad 20·5–23 (21·5) ; 4 ♂ imm 20·5–21·5 (21·1) ; 3 ♀ ad 21–22 (21·3) ; 3 ♀ imm 20–21 (20·3).

Iris very dark brown. *Bill* black ; some imm mandibles partly grey, gape dull flesh. *Foot* black, shanks somewhat fuscous.

(M. 108) *Monarcha castaneiventris castaneiventris* Verreaux, 1858

REFERENCES. Ramsay, 1879*a* : 79 (*rufocastanea*). See Mayr, 1942 : 81.

RANGE. Choiseul, Ysabel, Florida Is., Guadalcanal, Malaita.

SPECIMENS. Guadalcanal : Tenaru 2 ♂ imm, 1 ♀ imm, 1 ? ad ; Betilonga 11 ♂ ad, 2 ♂ imm, 2 ♀ ad, 3 ♀ imm, 1 ? ad ; Turipava 1 ♂ ad, 1 ♀ ad. 1 ♂ ad to OUM.

Weight 12 ♂ ad 22·5–27 (24·6) ; 4 ♂ imm 25–28·5 (26·4) ; 3 ♀ ad 22·5–25 (23·8) ; 4 ♀ imm 21·5–24 (22·8). *Wing* 10 ♂ ad 82·5–88 (84·7) ; 4 ♂ imm 81·5–83·5 (82·5) ; 3 ♀ ad 83–84·5 (83·8) ; 4 ♀ imm 79–82 (80·7). *Tail* 10 ♂ ad 66–75·5 (70·8) ; 4 ♂ imm 67–69 (67·7) ; 3 ♀ ad 67·5–73·5 (69·8) ; 4 ♀ imm 67–69·5 (68·0). *Bill* 12 ♂ ad 18·5–21 (20·0) ; 4 ♂ imm 20–21 (20·6) ; 3 ♀ ad 19·5–21 (20·0) ; 4 ♀ imm 19·5–21 (20·0).

Iris dark brown. *Bill* silvery blue-grey, occasionally streaked with black, sometimes paler towards tip and edges, tip blackish. *Foot* blue-grey.

Immature and adult birds seem to be much less distinct in this race than in *megarhynchus*, and are here separated tentatively. Both in this series and in 5 males and 3 females in the BM(NH), all the specimens are intermediate, in colour and texture of wing and tail and shape of rectrices, between adults and immatures of *megarhynchus*. Some of the males which appear the most juvenile had enlarged testes. There is some overlap between the sexes, but the females average much less glossy above, especially on rump, wings and tail.

(M. 108) *Monarcha castaneiventris megarhynchus* Rothschild & Hartert, 1908

REFERENCES. Rothschild & Hartert, 1908*b* : 363. See Mayr, 1942 : 81.

RANGE. San Cristoval.

SPECIMENS. San Cristoval : Goge 20 ♂ ad, 5 ♂ imm, 13 ♀ ad, 6 ♀ imm, 3 ? ad, 9 ? imm. 1 ♂ ad to OUM.

Weight 20 ♂ ad 25–28·5 (26·2) ; 3 ♂ imm 25–27·5 (26·2) ; 11 ♀ ad 22–33 (25·0) ; 4 ♀ imm 23–25·5 (24·2). *Wing* 19 ♂ ad 83–91·5 (87·6) ; 5 ♂ imm 80–88·5 (82·9) ; 13 ♀ ad 81–86·5 (83·8) ; 6 ♀ imm 78–81·5 (79·6). *Tail* 18 ♂ ad 73·5–81·5 (77·6) ; 5 ♂ imm 73·5–80 (76·0) ; 13 ♀ ad 70–78 (74·9) ; 6 ♀ imm 70–74 (71·7). *Bill* 17 ♂ ad 23–25·5 (24·3) ; 4 ♂ imm 23·5–24 (23·7) ; 12 ♀ ad 22–24 (23·0) ; 6 ♀ imm 22–24 (23·0).

Iris dark to very dark brown. *Bill* pale blue-grey, whitish distally and sometimes towards edges, tip and sometimes edges blackish. *Foot* blue-grey, often dark especially on toes.

Immatures are readily distinguished from adults by their softer and browner wings and tails, roundedly-pointed rectrices, and blackish brown upper wing-coverts (not dull black with a slight blue gloss at the edges). Their bills were adult in coloration, but one male, with enlarged testes (noted in the field as " ! somewhat autolysed, but recognisable ") and adult plumage, had the bill black with pinkish-white base and pale yellow gape. There is no appreciable sexual dimorphism in this series.

(M. 108) ***Monarcha castaneiventris ugiensis*** (Ramsay, 1881)

References. Ramsay, 1882*e* : 128. See Mayr, 1942 : 81.

Range. Ugi, Three Sisters, Santa Ana.

Specimens. Ugi 9 ♂ ad, 2 ♂ imm, 7 ♀ ad, 2 ♀ imm, 1 ? ad, 2 ? imm. 1 ♂ ad to OUM.

Weight 9 ♂ ad 28·5–33·5 (31·6) ; 2 ♂ imm 26·5, 27·5 ; 7 ♀ ad 28–30·5 (28·9) ; 2 ♀ imm 27·5, 28. *Wing* 8 ♂ ad 89–95·5 (92·2) ; 2 ♂ imm 85·5, 86 ; 5 ♀ ad 85–88 (86·1) ; 2 ♀ imm 81·5, 82. *Tail* 9 ♂ ad 77–83·5 (80·5) ; 2 ♂ imm 78·5, 79 ; 6 ♀ ad 73·5–76·5 (75·4) ; 2 ♀ imm 70·5, 74·5. *Bill* 8 ♂ ad 25–26·5 (25·9) ; 2 ♂ imm 25, 26 ; 6 ♀ ad 24–26 (24·9) ; 2 ♀ imm 25, 25·5.

Iris very dark brown. *Bill* pale bluish grey, whitish distally, tip blackish ; imm more or less overlaid with black especially distally, gape dull yellow. *Foot* bluish grey, shank paler ; imm more blackish.

The belly and under tail-coverts average distinctly duller in the females than the males, though there is no sexual difference in those areas which are black in other races. The belly is slightly glossy in all the males, but in females it is sometimes decidedly brownish with shafts whitish to the tips. Among the immature birds, the two females seem older than the two males and two unsexed specimens, in having had the bill of adult coloration (except that the gape of one was " greyish flesh ") rather than black with dull yellow gape. However, they are less glossy in plumage, and have the white shafts of the belly-feathers extended and becoming tawny at the tips, with tawny tips to the feathers themselves, especially near the crissum. These tips are extensive in the pale-gaped specimen so that the whole lower belly appears dull tawny. It seems probable that tawny-fringed belly-feathers are characteristic of immature females. Two rufous-bellied specimens have been reported (Davidson, 1934 : 195 ; Mayr, 1942 : 81). In the latter at least, the appearances is as in adults of *megarhynchus*, not at all as in our immature females (P. Vaurie, *in litt.*).

(M. 109) ***Monarcha barbatus barbatus*** Ramsay, 1879

References. Ramsay, 1879*a* : 80 ; Rothschild & Hartert, 1901*b* : 182 ; 1905 : 262 ; 1908*a* : 357 (*brodei*) ; Mayr, 1931*f* : 23.

Range. Bougainville, Choiseul, Ysabel, Florida Is., Guadalcanal.

Specimens. Guadalcanal : Betilonga 6 ♂ ad, 6 ♀ ad, 2 ♀ imm, 2 ? imm. 1 ♂ ad, 1 ? imm to OUM.

Weight 6 ♂ ad 20–23 (21·5) ; 7 ♀ ad 19–21·5 (20·5) ; 2 ♀ imm 19·5, 20. *Wing* 4 ♂ ad 79–83 (80·9) ; 6 ♀ ad 75–79·5 (77·3) ; 2 ♀ imm 72, 78·5. *Tail* 5 ♂ ad 70–73 (71·6) ; 5 ♀ ad 64–73 (67·4) ; 1 ♀ imm 69. *Bill* 4 ♂ ad 17–17·5 (17·1) ; 5 ♀ ad 16·5–17·5 (16·7) ; 2 ♀ imm 16, 16·5.

Iris dark brown. *Bill* silvery blue-grey, whitish distally and along edges, tip and occasionally edges blackish ; imm more or less overlaid with black. *Foot* blue-grey, sole yellowish.

All but one of these specimens, and all those in the BM(NH), are either clearly adult or in the pale rufous-washed immature plumage. However, BM(NH) no. 1959.21.799 appears to be an immature female in an advanced plumage. It resembles immatures of *M. vidua* in being generally similar to adults, but with wing and tail somewhat brownish and of juvenile shape and texture, the black throat-patch less scaly, and the gloss duller. Unfortunately, the puzzling juvenile plumages of this species have not yet been reviewed (see Mayr, 1931*f* : 23).

NOTES. At first sight, the black-tipped white outer rectrices of *M. b. malaitae*, reversing the common condition in the *verticalis* superspecies, suggest a marked genetic difference. However, close inspection, especially of juveniles, shows that the change is produced by a distalwards shift of the tail pattern, with enlargement of the normally small white basal area. This confirms the suggestion of its geographical distribution, that the character is readily acquired : it is found on Buru, Kei, Biak, the Admiralty group and Malaita (*loricatus*, *leucurus*, *brehmii*, *coultasi*, *infelix* and *malaitae*). Clearly *malaitae* is properly associated with *barbatus*. On the other hand, it does not seem appropriate to separate the races of the New Georgia Group as a distinct species, *R. browni*, despite Mayr (1955 : 27). This arrangement reflects the geography rather than the affinities of the forms concerned, since they differ from *barbatus* in relatively trivial characters and do not form a homogeneous group. They are large and somewhat melanic, but *browni* + *meeki* is black-breasted, *nigrotectus* is black-winged, and *ganongae* is closest in pattern to *barbatus*.

(M. 109) ***Monarcha vidua vidua*** (Tristram, 1879)

REFERENCES. Ramsay, 1880 : 468 (*melanocephalus*).

RANGE. San Cristoval, Santa Ana.

SPECIMENS. San Cristoval : Goge 8 ♂ ad, 7 ♂ imm, 1 ♂ juv, 13 ♀ ad, 4 ♀ imm, 8 ? ad, 4 ? imm, 1 ? juv ; Nagasi 5 ♂ ad, 2 ♂ imm, 5 ♀ ad, 2 ♀ imm, 1 ? ad, 1 ? imm. 1 ♂ ad, 1 ♀ imm to OUM ; 1 ♂ imm to AMNH.

Weight 11 ♂ ad 16–19·5 (17·4) ; 9 ♂ imm 15·5–17·5 (16·7) ; 1 ♂ juv 15 ; 19 ♀ ad 16–18 (16·8) ; 6 ♀ imm 15·5–18 (16·7). *Wing* 13 ♂ ad 74–83 (78·7) ; 7 ♂ imm 74–79 (76·0) ; 1 ♂ juv 73·5 ; 17 ♀ ad 72·5–79 (75·2) ; 4 ♀ imm 70–73 (71·6). *Tail* 12 ♂ ad 68–76·5 (71·6) ; 7 ♂ imm 68–78·5 (72·9) ; 1 ♂ juv 69 ; 13 ♀ ad 67–72 (70·8) ; 5 ♀ imm 65·5–71 (68·7). *Bill* 13 ♂ ad 16–17 (16·2) ; 7 ♂ imm 15·5–16·5 (16·1) ; 1 ♂ juv 16 ; 16 ♀ ad 15·5–16·5 (16·0) ; 6 ♀ imm 15·5–16·5 (15·9).

Iris very dark brown ; juv dark grey. *Bill* blue-grey, usually pale especially distally, tip and more or less of edges black, occasional black patches in front of nostrils (especially ♀) ; imm range from ad to juv condition ; juv black, gape flesh-coloured, yellow internally. *Foot* blue-grey, sometimes dark especially on toes ; juv paler.

Even the juveniles are generally similar to the adults in plumage coloration, not pale and rufous as in *M. barbatus*. They differ from adults in their soft parts, and in softer plumage, differently-shaped and browner wings and tails, brownish mantle-feathers with little black at the tips, and unspecialized dull black throat-feathers. The immatures have juvenile wings and tails, but otherwise resemble adults—except that their throat-feathers are less specialized, their greater upper wing-coverts have the black outer edges obsolescent, and their gloss is greener and somewhat duller. There are no specimens of *vidua* or *squamulatus* in a pale and rufous plumage, in the AMNH (P. Vaurie, *in litt.*) or BM(NH).

NOTES. It is remarkable that the uncharacteristic non-adult plumages of *vidua* and *squamulatus* have not previously been pointed out. Rothschild & Hartert (1908*b* : 363) suggested it in their remark that the " females " of *vidua* did not differ from the males ; but their views on the existence of sexual dimorphism in the pied monarchs fluctuated (1901*b* : 183 ; 1901*c* : 374 ; Hartert, 1908 : 107).

Even supposing a constant minority of immature *barbatus* to show an advanced plumage like that of *vidua*, it seems likely that juveniles of that and most other pied monarchs are always pale and rufous. Thus the juvenile plumage presents a striking difference between *barbatus* and *vidua*. In addition, these forms differ in adult pattern as radically as many of the representative forms currently separated as species. Indeed they have little in common, and *vidua* agrees rather with other members of the superspecies in having the nape and rump white and the sides of the throat black. Despite Mayr (1955 : 27), it does not seem possible to unite *vidua* with *barbatus* while they are specifically separated from their relatives in the Bismarcks and beyond.

(M. 109) ***Monarcha vidua squamulatus*** (Tristram, 1882)

REFERENCES. Tristram, 1882 : 136.

RANGE. Ugi.

SPECIMENS. Ugi 10 ♂ ad, 2 ♂ imm, 1 ♂ juv, 7 ♀ ad, 2 ♀ imm, 1 ♀ juv, 4 ? ad, 2 ? imm, 2 ? juv. 1 ? ad, 1 ? imm to OUM; 1 ♀ imm to AMNH.

Weight 10 ♂ ad 16–19·5 (17·7) ; 2 ♂ imm 18, 19 ; 1 ♂ juv 19·5 ; 7 ♀ ad 15·5–18 (16·9) ; 2 ♀ imm 16, 17·5 ; 1 ♀ juv 18. *Wing* 10 ♂ ad 73·5–79·5 (76·2) ; 2 ♂ imm 73·5, 75 ; 1 ♂ juv 75 ; 7 ♀ ad 73–76 (74·2) ; 2 ♀ imm 75·5, 76 ; 1 ♀ juv 69·5. *Tail* 8 ♂ ad 65·5–70 (68·3) ; 1 ♂ imm 69 ; 1 ♂ juv 69 ; 7 ♀ ad 64·5–68·5 (67·3) ; 2 ♀ imm 67, 68 ; 1 ♀ juv 65·5. *Bill* 9 ♂ ad 16·5–17 (16·7) ; 2 ♂ imm 17, 17 ; 1 ♂ juv 17 ; 7 ♀ ad 16–17 (16·6) ; 2 ♀ imm 17, 17 ; 1 ♀ juv 16·5.

Iris very dark brown (including juv). *Bill* bluish grey, paler distally, tip and occasionally distal edges black ; imm between ad and juv conditions ; juv black, base of mandible grey or horn, gape dull yellow. *Foot* bluish grey ; juv sometimes paler.

This race is a melanistic derivative of *M. vidua*, and shows the same difference between plumages. The melanization affects the breast, wingpatch and nape, the rump slightly, but not the tail tips. It is very variable in degree, and the most highly melanic specimens have black breasts and upper wing-coverts with narrow white shaft-streaks, no white collars, and somewhat narrowed white rump-patches. This variation is shown in all plumages.

(M. 110) ***Myiagra ferrocyanea ferrocyanea*** Ramsay, 1879

REFERENCES. Ramsay, 1879*a* : 78 & 79 (+*pallida*) ; Rothschild & Hartert, 1905 : 261 ; 1908*a* : 357 ; Mathews, 1928 : 373 ; Mayr, 1931*f* : 24.

RANGE. Choiseul, Ysabel, Florida Is., Guadalcanal.

SPECIMENS. Guadalcanal : Tenaru 3 ♂ ad, 1 ♂ imm, 1 ♀ ad ; Betilonga 17 ♂ ad, 9 ♀ ad, 2 ♀ imm, 1 ? imm. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 21 ♂ ad 11·5–14 (12·9) ; 1 ♂ imm 12 ; 10 ♀ ad 10–14·5 (12·6) ; 2 ♀ imm

12·5, 13. *Wing* 19 ♂ ad 63–71 (68·6) ; 1 ♂ imm 67 ; 10 ♀ ad 64–68·5 (66·3) ; 2 ♀ imm 67, 67. *Tail* 19 ♂ ad 58·5–62·5 (60·6) ; 1 ♂ imm 60·5 ; 8 ♀ ad 58–61 (59·7) : 2 ♀ imm 59·5, 59·5. *Bill* 18 ♂ ad 15·5–17·5 (16·3) ; 8 ♀ ad 14·5–16·5 (15·9) ; 1 ♀ imm 16·5.

Iris dark to very dark brown. *Bill* silvery grey-blue, tip and edges black, maxilla sometimes streaked with black, especially along culmen and in front of nostril ; imm from more or less black with greyish base and yellow gape, to ad condition. *Foot* dark grey to black.

The immatures are like adult females in body-plumage, but have softer wings and tails with more pointed rectrices, bills decidedly brownish in the dried skin, and wing-feathers with darker and browner centres more sharply marked off from the broader fawn edges. The adults vary considerably in shape, texture and colour of wing and tail, and the females in amount of buff on the underparts ; but no distinct phases are separable. The adult males, in somewhat worn plumage, are less purple in body-gloss than fresher BM(NH) specimens.

(M. 110) ***Myiagra cervinicauda*** Tristram, 1879

REFERENCES. Tristram, 1879 : 439 ; Ramsay, 1882*a* : 726 ; Rothschild & Hartert, 1908*a* : 357 ; 1908*b* : 363.

RANGE. San Cristoval, Ugi, Santa Ana.

SPECIMENS. San Cristoval : Manewiriwiri 2 ♂ ad, 1 ♀ ad, 1 ♀ imm ; Goge 2 ♂ ad, 5 ♂ subad, 2 ♂ imm, 1 ♀ ad, 2 ♀ imm, 1 ? imm ; Nagasi 1 ♂ ad. Ugi 11 ♂ ad, 1 ♂ imm, 5 ♀ ad, 1 ♀ imm, 2 ? imm. 1 ♂ ad, 1 ♀ ad to OUM.

Weight San Cristoval 5 ♂ ad 10·5–12 (10·9) ; 5 ♂ subad 9·5–11 (10·6) ; 2 ♂ imm 10·5, 10·5 ; 1 ♀ ad 13 ; 3 ♀ imm 10–11 (10·5) ; Ugi 12 ♂ ad 11–13 (11·7) ; 1 ♂ imm 11 ; 5 ♀ ad 10–12 (11·1) ; 1 ♀ imm 10·5. *Wing* San Cristoval 4 ♂ ad 62·5–64·5 (63·6) ; 4 ♂ subad 64–66·5 (64·9) ; 2 ♂ imm 62·5, 63 ; 1 ♀ ad 62 ; 3 ♀ imm 58–62·5 (60·0) ; Ugi 11 ♂ ad 63·5–67 (65·7) ; 1 ♂ imm 64·5 ; 5 ♀ ad 61·5–64 (62·7) ; 1 ♀ imm 61. *Tail* San Cristoval 4 ♂ ad 56–59 (57·7) ; 3 ♂ subad 56–59 (57·7) ; 3 ♀ imm 55–60 (57·3) ; Ugi 7 ♂ ad 55–58·5 (57·3) ; 1 ♂ imm 58·5 ; 5 ♀ ad 54·5–57 (55·9) ; 1 ♀ imm 57·5. *Bill* San Cristoval 4 ♂ ad 16·5–17·5 (17·0) ; 4 ♂ subad 16–17 (16·6) ; 2 ♂ imm 16·5, 17 ; 1 ♀ ad 16 ; 3 ♀ imm 15–16·5 (15·8) ; Ugi 9 ♂ ad 16–17·5 (16·8) ; 1 ♂ imm 16·5 ; 4 ♀ ad 16–16·5 (16·1) ; 1 ♀ imm 17.

Iris very dark brown. *Bill* dark or dull blue-grey, tip and edges and sometimes culmen black, maxilla occasionally more or less black ; imm average more black. *Foot* blackish, shank dark blue-grey.

The immatures differ from adult females in the texture and shape of wing and tail, and in the colour of the dried bill. The females and immatures vary considerably in the intensity of rufous above and below, but without any apparent correlation with age. The males also vary markedly, in the shape, colour and texture of wing and tail, and in the colour and intensity of gloss. Five males, separated as subadults, have soft wings with pale edges to the inner feathers, pointed tails, duller gloss above and greener gloss on the throats (though this may be due to wear). However, they do not differ from adults in testis development and bill colour, while several males are intermediate in character.

NOTES. The genus *Myiagra* forms a single superspecies distributed from the Lesser Sunda Isles to Samoa, yet curiously absent as breeding populations from the Bismarcks and most of New Guinea. Cain (1956*a* : 106) gives a brief account based on a review by I. C. J. G. A satisfactory species arrangement is made difficult by the overlap between very similar forms (especially *rubecula* and *cyanoleuca* in Australia) and the extreme variation between representative isolated forms, together with striking convergences made possible by a limited repertoire of variation. Mayr's arrangement (1941*a* ; 1945*a*) is not consistent, as is seen especially in the aggregation of very distinct Micronesian forms into a single " species " *M. oceanica*, while the Polynesian forms *caledonica*, *vanikorensis* and *albiventris* are separated. It might be most satisfactory to combine the majority of forms in a single polytypic species (*M. rubecula*) from the Moluccas to Samoa and Micronesia to Australia, sympatric with three other species, *M. ruficollis*, *M. cyanoleuca* and *M. azureocapilla*. However, the specific separation of distinct representatives is here accepted, though Mayr's arrangement for the Solomons does not seem satisfactory. The inclusion of *cervinicauda* in *M. ferrocyanea* emphasizes their geography rather than their characters, since *cervinicauda* resembles the Southern Melanesian forms *vanikorensis* and *caledonica* at least as closely, in coloration and bill-form. It seems to be rather distinct from both groups in ecology, in its confinement to the canopy and avoidance of the substage and second growth (Cain & Galbraith, 1956 : 275), and is best treated as a distinct species.

(M. 111) ***Petroica multicolor dennisi*** Cain & Galbraith, 1955

REFERENCES. Cain & Galbraith, 1955 : 93. See Mayr, 1934*b*.

RANGE. Guadalcanal (mountains).

SPECIMENS. Guadalcanal : Turipava 6 ♂ ad, 3 ♂ ad retarded, 3 ♀ ad, 1 ♀ imm. 1 ♂ ad, 1 ♀ ad to AMNH.

Weight 6 ♂ ad 10–11 (10·3) ; 3 ♂ ad ret 10·5–11 (10·7) ; 3 ♀ ad 11–14·5 (12·3) ; 1 ♀ imm 10. *Wing* 6 ♂ ad 62·5–64·5 (63·5) ; 3 ♂ ad ret 60·5–66 (62·7) ; 3 ♀ ad 62–62·5 (62·2) ; 1 ♀ imm 62·5. *Tail* 5 ♂ ad 39·5–44·5 (42·1) ; 2 ♂ ad ret 41·5, 42 ; 3 ♀ ad 41–42·5 (42·0) ; 1 ♀ imm 42·5. *Bill* 5 ♂ ad 13·5–14·5 (13·9) ; 2 ♂ ad ret 14, 14 ; 3 ♀ ad 14–14 (14·0) ; 1 ♀ imm 14.

Iris dark brown. *Bill* maxilla black, mandible horn-colour to blackish, paler basally. *Foot* dark brown to dull orange-yellow, fuscous-tinged, sole yellow to orange.

The holotype (adult female, expedition no. 520) is BM(NH) reg. no. 1959.21.957.

The three adult males in retarded plumage have enlarged testes. They differ from those in advanced plumage in having the crown blackish-brown (with white traces on the forehead), the wing and especially the primary-coverts browner, the outer coverts brown not white, the white edges of the secondaries washed with ochraceous, and the throat and mantle somewhat brownish.

(M. 111) *Petroica multicolor polymorpha* Mayr, 1934

REFERENCES. Mayr, 1934*b* : 11.

RANGE. San Cristoval (mountains).

(M. 112) **Pachycephala pectoralis cinnamomea** (Ramsay, 1879)

References. Mayr, 1932*c* : 14. See Galbraith, 1956.

Range. Guadalcanal, Beagle.

Specimens. Guadalcanal : Betilonga 18 ♂ ad, 2 ♂ imm, 8 ♀ " ad ", 1 ? imm, 1 ? juv. 1 ♀ " ad " to AMNH ; 1 ♂ ad, 1 ♀ " ad " to OUM.

Weight 18 ♂ ad 48–56 (51·7) ; 2 ♂ imm 45, 48 ; 8 ♀ " ad " 42–47·5 (44·9). *Wing* 16 ♂ ad 100·5–105·5 (103·1) ; 1 ♂ imm 99 ; 8 ♀ " ad " 93·5–102 (98·1). *Tail* 16 ♂ ad 74–79·5 (76·3) ; 2 ♂ imm 71·5, 81 ; 8 ♀ " ad " 70·5–77·5 (74·5). *Bill* 15 ♂ ad 21·5–24 (22·9) ; 2 ♂ imm 23, 24 ; 8 ♀ " ad " 21–24 (22·3).

Iris grey more or less suffused with red, yielding brownish grey to rufous brown, sometimes blotched or veined. *Bill* ♂ ad black ; ♂ imm and ♀ horn-colour, usually darker and greyer above, sometimes streaked with black ; juv paler and yellower, gape yellow. *Foot* grey, more or less tinged with bluish and/or fuscous, ♀ averages paler ; juv whitish, tinged with fuscous and blue in patches.

Males in the " II Phase " plumage (Mayr, 1932*c* & *d*) are here considered as immatures, which in this species have apparently already passed through a moult of the wing and tail. They (and corresponding specimens of *christophori*) are extremely variable in tail-shape, which suggests that the onset of moult is not well co-ordinated with the maturation of the gonads and feather-follicles. The series of " adult " females probably includes some immatures, but these are apparently not recognizable. Unlike the 7 corresponding specimens described by Mayr (1932*c*) and 3 in the BM(NH), 5 of the 8 non-juvenile females are strongly washed with yellow pigment. It remains to be determined, whether yellow coloration is confined to undetected immature females (as an exception to the general rule that younger birds have less carotenoid) ; or whether the character is more variable in expression than Mayr's material had suggested. Since *cinnamomea* and *bougainvillei* differ consistently from *orioloides* only in this character, and from each other only in presence or absence of a rufous wash (which is variably developed in *orioloides*), proof of the latter would necessitate the union in a single subspecies, *P. p. orioloides*, of all the populations along the Main Chain from Buka to Guadalcanal—which are certainly very closely related.

Notes. The name *Muscicapa pectoralis* Latham, 1801, has been validated by the International Commission (ICZN 1956 ; 1958) ; and so remains the name for this polytypic species whether or not the New Caledonian form, to which the name *Muscicapa caledonica* Gmelin, 1789 applies, is included (see Galbraith, 1956 : 174).

(M. 112) **Pachycephala pectoralis christophori** Tristram, 1879

References. Mayr, 1932*c* : 19. See Galbraith, 1956.

Range. San Cristoval, Santa Ana.

Specimens. San Cristoval : Goge 23 ♂ ad, 8 ♂ imm, 1 ♂ juv, 16 ♀ " ad ", 2 ♀ juv, 2 ? imm, 4 ? juv, 1 ? nest ; Nagasi 18 ♂ ad, 4 ♂ imm, 5 ♀ " ad ", 1 ? imm, 2 ? juv, 1 ? nest. 2 ♂ ad, 1 ♀ " ad " to OUM.

Weight Goge 23 ♂ ad 28–36 (33·3) ; 9 ♂ imm 28–33 (30·7) ; 1 ♂ juv 31·5 ; 16 ♀ " ad " 28–37·5 (31·8) ; 2 ♀ juv 31, 32 ; Nagasi 18 ♂ ad 32–35·5 (33·9) ; 4 ♂ imm 29–33 (31·7) ; 5 ♀ " ad " 31–36 (33·6). *Wing* Goge 22 ♂ ad 81–90 (85·4) ; 7 ♂ imm 80–85

(82·8) ; 1 ♂ juv 84 ; 16 ♀ " ad " 80–89 (84·2) ; 2 ♀ juv 80, 80·5 ; Nagasi 18 ♂ ad 85–90 (87·0) ; 4 ♂ imm 81·5–86 (84·2) ; 5 ♀ " ad " 83–89 (86·3). *Tail* Goge 19 ♂ ad 54·5–63·5 (59·1) ; 4 ♂ imm 56–61·5 (58·6) ; 12 ♀ " ad " 57·5–64 (59·9) ; 2 ♀ juv 56, 59·5 ; Nagasi 13 ♂ ad 57·5–62·5 (59·8) ; 3 ♂ imm 60–61·5 (60·3) ; 4 ♀ " ad " 58–62·5 (59·9). *Bill* Goge 19 ♂ ad 20–21·5 (20·7) ; 8 ♂ imm 20–21·5 (20·8) ; 1 ♂ juv 18·5 ; 15 ♀ " ad " 20·5–22 (20·8) ; 2 ♀ juv 21·5, 22 ; Nagasi 18 ♂ ad 20–22·5 (21·1) ; 4 ♀ imm 20·5–21·5 (21·1) ; 5 ♀ " ad " 20–21·5 (20·8).

Iris grey more or less suffused with red, yielding brownish grey to rufous brown, sometimes blotched or veined ; juv greyer. *Bill* ♂ ad black, base of mandible often paler, gape black to whitish or yellow, mouth-lining whitish to bright orange-yellow, sometimes blotched or rimmed with black ; other specimens maxilla blackish to dark greyish horn, mandible paler and yellower, often streaked, gape and mouth-lining never black. *Foot* grey, more or less tinged with bluish or brownish, sometimes in irregular patches.

In this series, there is scarcely any overlap in bill-colour and testis-development between the 41 adult males and the 12 males in " II Phase " plumage, listed above as immatures. The latter clearly cannot be adults in a retarded plumage, even if this is the explanation for such specimens in other races (Mayr, 1932*c* & *d*). The rectrices of these immatures differ in shape and texture from those of juveniles, and in average colour (with little overlap) from those of adults. It thus appears that an additional moult of the tail, and probably of the wing, is involved.

There is an unusual degree of overlap in this race, in the appearance of the wing, between the various plumage phases. The wing of nestlings and juveniles (" I Phase ") is firm in texture (only the upper coverts being markedly soft) and much mixed with olive, which sometimes extends far up the edges of the secondaries. Conversely, several adult males and specimens of both sexes in " II Phase " have much rufous in the secondaries and upper coverts.

Presumably, females in " II Phase " include adults and immatures, but it seems impossible to separate them. The immature males are also indistinguishable—except for one which (like two recorded by Mayr, 1932*c*) has a distinct gorget of irregularly-marked black-and-yellow feathers. This approaches the condition in some adults (with black bills, enlarged testes and blacker tails) which have the gorget much mixed with yellow. Otherwise, the gorget in " II Phase " is very variable in colour, from olivaceous or tawny yellow to olive.

The variable degree of melanization of the adult male is correlated, though imperfectly, between the head and tail, but is apparently independent of the development of rufous on the breast. In contrast, the Santa Ana population (Mayr, 1932*c*) is much more constant in both characters, having the head and tail mostly green and the breast with much rufous.

(M. 113) ***Pachycephala implicata implicata*** Hartert, 1929

REFERENCES. Mayr, 1932*c* : 1.

RANGE. Guadalcanal (mountains).

SPECIMENS. Guadalcanal : Turipava 7 ♂ ad, 1 ♂ imm, 1 ♂ juv, 12 ♀ ad, 1 ♀ juv. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 7 ♂ ad 33·5–37 (35·7) ; 1 ♂ imm 33 ; 1 ♂ juv 29·5 ; 13 ♀ ad 30–39 (33·3) ; 1 ♀ juv 32. *Wing* 7 ♂ ad 86·5–91 (89·1) ; 1 ♂ imm 88·5 ; 12 ♀ ad 84–88 (86·8) ; 1 ♀ juv 83. *Tail* 6 ♂ ad 69–72 (70·2) ; 11 ♀ ad 67–72 (68·7) ; 1 ♀ juv 67. *Bill* 4 ♂ ad 19–20 (19·4) ; 1 ♂ imm 19 ; 1 ♂ juv 14 ; 8 ♀ ad 18·5–20 (19·2).

Iris dark brown, sometimes reddish, ♀ greyish ; juv dark grey-brown. *Bill* black ; juv fuscous (mandible and base paler) with pale yellow gape, or black with yellowish edges. *Foot* grey, usually bluish, shank darker and sometimes mottled ; ♀ average paler ; juv shanks pale blue-grey, toes ivory with bluish tinge, or as ad.

The male juvenile, with small pale bill and feet and growing wing and tail, agrees with Mayr's (1932*c*) description of nestling *richardsi*. The female juvenile, evidently older, is much less rufous, though a small patch of the yellow immature plumage on the breast shows it not to have undergone a complete moult. The adult females also vary greatly in degree of phaeomelanization ; especially on the rump, wing, tail and underparts.

(M. 114) **Aplonis cantoroides** (Gray, 1862)

REFERENCES. *Cat. Birds B.M.* 13 : 128 ; Heinroth, 1903 : 74.

RANGE. New Guinea region and Northern Melanesia—including Ugi, Three Sisters and Santa Ana, but not San Cristoval (coasts).

SPECIMENS. Guadalcanal : Tenaru 1 ♂ ad, 3 ♂ imm, 2 ♀ ad, 10 ♀ imm, 1 ♀ juv, 1 ? juv. Ugi 7 ♂ ad, 1 ♂ imm, 7 ♀ ad, 1 ♀ juv. 1 ♀ ad, 1 ♀ imm to OUM.

Weight Guadalcanal 1 ♂ ad 53·5 ; 3 ♂ imm 52·5–53 (52·7) ; 2 ♀ ad 53·5, 58 ; 10 ♀ imm 43–53·5 (48·8) ; 1 ♀ juv 44 ; Ugi 8 ♂ ad 51·5–59 (54·9) ; 1 ♂ imm 53 ; 7 ♀ ad 50·5–56 (53·4) ; 1 ♀ juv 50·5. *Wing* Guadalcanal 1 ♂ ad 100 ; 3 ♂ imm 96–97·5 (96·8) ; 2 ♀ ad 98, 98·5 ; 10 ♀ imm 91–99 (94·1) ; 1 ♀ juv 91·5 ; Ugi 7 ♂ ad 100–105·5 (102·0) ; 1 ♂ imm 96 ; 7 ♀ ad 96–101 (98·7) ; 1 ♀ juv 96. *Tail* Guadalcanal 1 ♂ ad 66 ; 3 ♂ imm 63–64 (63·7) ; 1 ♀ ad 64 ; 9 ♀ imm 56·5–65 (59·1) ; 1 ♀ juv 50·5 ; Ugi 6 ♂ ad 65–70 (67·4) ; 1 ♂ imm 63 ; 6 ♀ ad 62–66 (64·1) ; 1 ♀ juv 52. *Bill* Guadalcanal 1 ♂ ad 24 ; 3 ♂ imm 23–24 (23·3) ; 2 ♀ ad 23·5, 23·5 ; 10 ♀ imm 21·5–24 (22·5) ; 1 ♀ juv 21 ; Ugi 6 ♂ ad 22–24·5 (23·3) ; 1 ♂ imm 23·5 ; 6 ♀ ad 22·5–23·5 (23·2) ; 1 ♀ juv 22.

Iris bright orange ; juv greenish yellow to dark brown. *Bill* black ; juv gape yellowish. *Foot* black, occasionally brownish-tinged ; juv dark grey, brownish-tinged, to black.

NOTES. Amadon (1956 : 22) regards the species as monotypic, and separates *crassa* of the Tenimber Isles as a representative species.

The immature and juvenile plumages are described by Heinroth (1903).

Though listed as " widespread " in the Solomons by Mayr (1945*a* : 277), the species has been recorded only twice from San Cristoval (Tristram, 1882 : 137 ; Davidson, 1934 : 194). There are no specimens from this island in the AMNH (Amadon *in litt.*) or the BM(NH). Natives of San Cristoval, even on the coast, denied knowledge of it ; whereas the inland people of Betilonga, where neither species occurs, were well aware of the distinction between *A. cantoroides* and *A. metallica*. French (*in litt.*) never saw *A. cantoroides* on his many visits to San Cristoval, nor were its eggs brought to him by the collectors he employed there. He does not believe that it can be resident. Tristram did not state the number of specimens, nor their precise locality. Davidson's single bird was taken at Star Harbour, and may well have been a straggler from Santa Ana (see p. 15).

The species was not taken on Malaita by the Whitney Expedition (Mayr, 1931*f*), but Davidson (1934) records a specimen, and there are 4 in the BM(NH) collected by R. A. Lever. The species is resident on Rennell (Bradley & Wolff, 1956 : 110), where the nesting sites recorded for *A. cantoroides* and *A. insularis* need confirmation.

(M. 116) ***Aplonis grandis macrura*** Mayr, 1931

REFERENCES. Mayr, 1931*f* : 21.

RANGE. Guadalcanal.

SPECIMENS. Guadalcanal: Tenaru 1 ♂ ad, 1 ♀ ad; Betilonga 13 ♂ ad, 19 ♀ ad, 1 ♀ imm, 1 ? ad, 1 ? imm. 1 ♂ ad, 1 ? imm to OUM.

Weight 15 ♂ ad 114·5–151 (136·4); 21 ♀ ad 110·5–150 (133·3); 1 ♀ imm 119. *Wing* 14 ♂ ad 132–146 (140·7); 19 ♀ ad 130–144 (136·4); 1 ♀ imm 134. *Tail* 12 ♂ ad 92·5–103 (98·3); 17 ♀ ad 87–99·5 (93·6); 1 ♀ imm 89. *Bill* 14 ♂ ad 26–29 (27·5); 9 ♀ ad 26–29 (27·3); 1 ♀ imm 27·5.

Iris deep red, sometimes orange-red; imm orange-red. *Bill* black. *Foot* black, sole sometimes yellowish.

The immatures differ relatively little from the adults, in having less gloss on the wing, the primaries dull brown and without fawn outer webs, the hackling of the head and neck greatly reduced (despite Rothschild & Hartert, 1905 : 268) and without green tinges in the purple gloss, and the gloss of the body duller and bluer and restricted to the tips of the feathers—so that the back appears scaly and the belly and under tail-coverts dull and brownish. Individual adults approach this condition in separate single characters.

(M. 116) ***Aplonis dichroa*** (Tristram, 1895)

REFERENCES. Ramsay, 1882*a* : 726 (*minor*).

RANGE. San Cristoval.

SPECIMENS. San Cristoval: Goge 7 ♂ ad, 4 ♂ imm, 8 ♀ ad, 1 ♀ imm, 3 ? imm; Nagasi 3 ♂ ad, 3 ♂ imm, 3 ♀ ad, 5 ♀ imm, 1 ? imm. 1 ♂ ad, 1 ♂ imm to OUM.

Weight 8 ♂ ad 82·5–90 (86·9); 7 ♂ imm 68–90 (76·6); 9 ♀ ad 73–91·5 (81·2); 6 ♀ imm 68–82 (74·1). *Wing* 8 ♂ ad 112–122 (117·9); 7 ♂ imm 108·5–118 (112·4); 11 ♀ ad 110–119 (113·5); 6 ♀ imm 109–116 (111·8). *Tail* 9 ♂ ad 71·5–76·5 (73·5); 3 ♂ imm 61·5–62·5 (62·0); 9 ♀ ad 66·5–72·5 (69·1); 4 ♀ imm 61·5–68 (64·7). *Bill* 10 ♂ ad 26–28 (26·9); 7 ♂ imm 25–28 (26·0); 11 ♀ ad 25–27 (26·0); 6 ♀ imm 24·5–26 (25·3).

Iris tawny orange (deep orange-red to pale tawny orange); imm pale golden-brown (dull yellow-brown to golden yellow with orange wash). *Bill* black; imm gape sometimes fuscous, yellow internally. *Foot* black.

The immature plumage differs from that of the adult much more than in our series of *A. grandis*. The upper wing-coverts are dark brown without gloss, the head and neck are without hackles, the contour feathers are fuscous with gloss only at the tips, and the rectrices are paler and narrower. However, the remiges are like those of the adult.

The proportion of young birds taken near Goge shows a striking change after the visit to Nagasi, where an intermediate proportion was taken. The numbers of immatures and adults in the collection are: Goge (15th October–13th November) 2/15; Nagasi (20–24th November) 9/6; Goge (30th November–3rd December) 6/0. This suggests that the young birds were moving about together apart from the adults, as in the related *A. cantoroides*; though the feeding flock seen was not noticed to be composed mainly of immatures (Cain & Galbraith, 1956 : 280).

NOTES. We agree with Amadon (1956 : 23) that this form should be kept specifically distinct from *A. grandis*, its representative in the remainder of the Solomons.

The identity of the third species of *Aplonis* on the Three Sisters, recorded in error by French (1957) as *A. grandis*, remains in doubt (see Cain & Galbraith, 1957, footnote). There is now no indigenous Melanesian population in these islands, who alone might be expected to distinguish between *A. cantoroides* and *A. feadensis* or *A. insularis*. However, through the kindness of the Chief Secretary to the High Commission and the District Commissioner, workers on the Lever estate were asked to observe, and after two months in 1957 reported only *A. cantoroides* and *A. metallica*. If able to distinguish these two species, they would immediately have recognized *A. grandis*, *A. dichroa* or *A. brunneicapilla*. If one of these species was present during Mr. French's residence, it cannot still be common as he recorded it.

(M. 117) ***Aplonis metallica nitida*** (Gray, 1858)

REFERENCES. Stresemann, 1912 : 311; 1914 : 151; Amadon, 1956 : 22.

RANGE. Bismarcks, Solomons (lowlands).

SPECIMENS. Guadalcanal: Tenaru 15 ♂ ad, 9 ♂ imm, 10 ♀ ad, 4 ♀ imm, 1 ? ad, 1 ? imm. San Cristoval: Goge 23 ♂ ad, 16 ♂ imm, 6 ♂ juv, 14 ♀ ad, 4 ♀ imm, 3 ? imm, 12 ? juv. Ugi 5 ♂ ad, 2 ♂ imm, 3 ♂ juv, 2 ♀ ad, 7 ♀ imm. All to OUM.

Weight Guadalcanal 15 ♂ ad 51·5–60·5 (55·7); 9 ♂ imm 50·5–60·5 (55·9); 10 ♀ ad 52–66·5 (57·1); 4 ♀ imm 47·5–52·5 (50·4); San Cristoval 19 ♂ ad 49–63·5 (58·7); 9 ♂ imm 48·5–61·5 (55·2); 6 ♂ juv 47·5–58 (53·1); 10 ♀ ad 47·5–57 (54·2); 3 ♀ imm 50–51 (50·7); Ugi 5 ♂ ad 52·5–60·5 (56·5); 2 ♂ imm 52, 55·5; 3 ♂ juv 44·5–53 (49·8); 2 ♀ ad 54·5, 57·5; 7 ♀ imm 46–57 (52·0). *Wing* Guadalcanal 15 ♂ ad 106–115 (110·4); 9 ♂ imm 99·5–108·5 (103·5); 10 ♀ ad 102–108 (105·3); 3 ♀ imm 96·5–100 (98·5); San Cristoval 23 ♂ ad 101·5–109·5 (106·0); 13 ♂ imm 95–109 (101·4); 6 ♂ juv 99·5–104·5 (102·9); 14 ♀ ad 98·5–107 (102·2); 3 ♀ imm 97·5–101 (98·8); Ugi 5 ♂ ad 106–109 (107·7); 2 ♂ imm 98·5, 100·5; 2 ♂ juv 98, 99·5; 1 ♀ ad 105; 5 ♀ imm 94·5–98·5 (96·8). *Tail* (central rectrices) Guadalcanal 13 ♂ ad 91–111·5 (102·5); 8 ♂ imm 82·5–95·5 (88·4); 10 ♀ ad 88–101·5 (93·2); 4 ♀ imm 79–88 (83·2); San Cristoval 19 ♂ ad 88·5–105 (97·1); 14 ♂ imm 83–94·5 (87·5); 5 ♂ juv 62–70 (67·2); 9 ♀ ad 80–93 (87·8); 4 ♀ imm 79–84·5 (81·2); Ugi 3 ♂ ad 99–106 (102·2); 2 ♂ imm 80·5, 92; 1 ♂ juv 68; 2 ♀ ad 89, 93; 5 ♀ imm 78–81·5 (79·6). *Tail* (2nd rectrices) Guadalcanal 13 ♂ ad 73·5–86 (79·9); 9 ♂ imm 58–75·5 (70·2); 10 ♀ ad

69–79·5 (73·4) ; 3 ♀ imm 57–68 (63·2) ; San Cristoval 21 ♂ ad 68·5–82 (75·3) ; 16 ♂ imm 62–76·5 (70·1) ; 5 ♂ juv 54·5–63 (58·3) ; 8 ♀ ad 65–75·5 (71·9) ; 4 ♀ imm 64–70·5 (66·9) ; Ugi 4 ♂ ad 76·5–81·5 (78·2) ; 2 ♂ imm 58·5, 73 ; 2 ♂ juv 54, 55 ; 2 ♀ ad 67, 71 ; 6 ♀ imm 63·5–69 (65·7). *Bill* Guadalcanal 14 ♂ ad 21·5–24·5 (22·8) ; 8 ♂ imm 20·5–24 (21·9) ; 10 ♀ ad 21·5–23·5 (22·3) ; 3 ♀ imm 21–22·5 (21·7) ; San Cristoval 22 ♂ ad 21–23·5 (22·0) ; 16 ♂ imm 21–23·5 (22·3) ; 7 ♂ juv 20·5–22·5 (21·4) ; 14 ♀ ad 20·5–23 (21·7) ; 4 ♀ imm 20–22 (21·1) ; Ugi 5 ♂ ad 21–23 (22·2) ; 2 ♂ imm 21·5, 22 ; 3 ♂ juv 20·5–21 (20·8) ; 2 ♀ ad 22, 22 ; 7 ♀ imm 21–23·5 (21·3).

Iris bright orange-red, often orange centrally, sometimes pinkish ; imm average yellower, juv golden buff through pale greenish brown to dark grey-brown in apparently youngest birds. *Bill* black ; juv gape fuscous to flesh, youngest birds have dull black maxilla, horn mandible with yellowish base and edges, golden-yellow gape. *Foot* black, sometimes fuscous.

The immatures have juvenile wings, but their tails (and that of one of the juveniles) are adult.

The series from San Cristoval is extremely variable in the colour of the gloss. Some specimens are more purplish than any others seen, with scarcely a trace of green when viewed with the light, as in individuals of *A. mystacea* ; while others are as greenish as any, having traces of purple on the shoulder only, as in *A. brunneicapilla*. Table II shows the distribution of adult specimens of both sexes among eight arbitrary colour-classes. The 24 specimens in the BM(NH), from 10 islands in the Bismarcks and Solomons, are grouped together, while all the specimens from Guadalcanal, San Cristoval and Ugi were collected by the expedition.

TABLE II.—*Colour of body gloss in adults of* Aplonis metallica nitida
Class A purplest, H greenest.

	A	B	C	D	E	F	G	H
Bismarcks and Solomons .			1	1	2	1	14	5
Guadalcanal . . .				2	3	11	9	1
San Cristoval . . .	1	2	6	6	6	6	9	1
Ugi				2	1		2	1

NOTES. The non-adult plumages are described by Stresemann (1914).

The character distinguishing *nitida* from *metallica* is not so much that the interscapular patch is reduced (Amadon, 1956), as that its central blue-green area is either totally abolished (Stresemann, 1912) or occasionally represented by a bluish tinge. Also, even very purplish individuals have the green throat less mixed with purple than have generally greener specimens of *metallica*.

(M. 118) ***Aplonis brunneicapilla*** (Danis, 1938)

REFERENCES. Beecher, 1945 : 31 ; Cain & Galbraith, 1956 : 281.

RANGE. Solomons—known from Bougainville and Guadalcanal ; 1 specimen from Rendova.

SPECIMENS. Guadalcanal : Betilonga 23 ♂ ad, 1 ♂ juv, 17 ♀ ad. 1 ♂ ad, 1 ♀ ad to AMNH ; 1 ♂ ad to OUM.

Weight 24 ♂ ad 59·5–76·5 (69·2) ; 1 ♂ juv 62·5 ; 18 ♀ ad 59–73·5 (64·2). *Wing* 22 ♂ ad 108·5–115 (112·9) ; 16 ♀ ad 106·5–114 (109·4). *Tail* (central rectrices) 11 ♂ ad 119·5–204·5 (150·5) ; 6 ♀ ad 98–133·5 (115·7). *Tail* (2nd rectrices) 22 ♂ ad 73·5–91 (80·1) ; 15 ♀ ad 68–81·5 (72·4). *Bill* 23 ♂ ad 25·5–28 (26·8) ; 1 ♂ juv 24 ; 17 ♀ ad 24·5–27 (25·5).

Iris white ; juv dark grey-brown. *Bill* black ; juv grey, maxilla dark with black base, mandible paler with ivory base, gape orange-yellow. *Foot* black, sole whitish or yellowish.

The juvenile at first sight resembles immatures of other species of *Aplonis*, in its firm glossy plumage with wings and tail of almost adult gloss and texture. However, the latter clearly do not belong to the adult feather-generation yet are still growing ; and the weak pale bill, dark iris and sparsely-feathered throat confirm that the specimen is in its first plumage.

Adults usually have little purple in the body gloss, but one adult male is mainly purple above, and several specimens are bronzy beneath. The distribution of gloss colours on the head and throat is reminiscent of that of *A. metallica purpureiceps* of Manus : an arc over the eye purple ; lores, superciliary and cheeks brilliant green ; the throat blue-green with purple mainly at the sides and across the chin and breast. In fresh plumage, the crest of the adult male (about 15 mm long) and the crown are glossy black with a brownish tinge, those of the female somewhat browner. They bleach in worn plumage to pale dull brown.

NOTES. This species has been compared and associated with *A. mystacea* of New Guinea lowlands (Amadon, 1943*b* : 16 ; 1956 : 22 ; Mayr, 1955 : 36). However, both are clearly related to the widespread *A. metallica*, and all three should be considered together. *A. brunneicapilla* outdoes *A. mystacea* in specialization of the head-feathering, pallor of the iris, arching of the bill, and suppression of the distinctive juvenile pattern. This last is a common trend in *Aplonis*, especially among long-established island populations. While *A. mystacea* is the smallest and purplest of the three species (retaining traces of the blue-green area in the interscapular patch, and adding a purple rump to the pattern shown by *A. m. metallica*), *A. brunneicapilla* is the largest and greenest, and its enormously developed tail-streamers are more like those of most races of *A. metallica*. On geographical grounds, it seems probable that *A. mystacea* and *A. brunneicapilla* are both derived from *A. metallica*, and owe their special resemblances to convergence.

(M. 119) ***Acridotheres tristis tristis*** (Linnaeus, 1766)

REFERENCES. Baker, 1926 : 53.

RANGE. Afghanistan through India to Thailand ; introduced to islands in the Solomons (coasts).

SPECIMENS. Guadalcanal : Tenaru 1 ♂ ad.

Weight 127·5. *Wing* 143. *Bill* 26.

Iris dirty white overlaid with reddish brown. *Skin* round eye orange yellow, eyelid blackish. *Bill* greenish yellow, base of mandible blackish. *Foot* dull yellow, greenish on claws and edges of scutes.

Notes. In the Solomons, known from the Russell Is. (Mayr, 1945*a* ; 1955 : 36), Guadalcanal (Davidson, 1929 : 259 ; Donaghho, 1950 : 129 ; Cain & Galbraith, 1956 : 287) and the Three Sisters (French, 1957).

(M. 120) ***Mino dumontii kreffti*** (Sclater, 1869)

References. Amadon, 1956 : 34.

Range. Bismarcks, Solomons except San Cristoval Group—irregular geographical variation in size.

Specimens. Guadalcanal : Betilonga 5 ♂ ad, 3 ♀ ad. 1 ♂ ad to OUM.

Weight 5 ♂ ad 182–200 (191) ; 4 ♀ ad 170–215 (189). *Wing* 5 ♂ ad 149–155 (153·3) ; 3 ♀ ad 146–150 (148·3). *Tail* 3 ♂ ad 97–100 (98·5) ; 3 ♀ ad 95–98·5 (96·7). *Bill* 5 ♂ ad 33–36·5 (34·4) ; 3 ♀ ad 31–33 (32·2).

Iris yellow. *Skin* round eye orange. *Bill* orange. *Foot* yellow to orange-yellow.

Notes. Amadon (1956) shows that the small birds of Guadalcanal and Malaita (*sanfordi* Hartert) are best combined with *kreffti*.

(M. 121) ***Dicrurus hottentottus meeki*** Rothschild & Hartert, 1903

References. Vaurie, 1949 : 291. See Mayr & Vaurie, 1948.

Range. Guadalcanal.

Specimens. Guadalcanal : Betilonga 4 ♂ ad, 4 ♀ ad, 1 ♀ imm, 1 ♀ juv, 1 ? imm. 1 ♂ ad to OUM.

Weight 4 ♂ ad 73·5–81·5 (78·1) ; 4 ♀ ad 79–86 (81·6) ; 1 ♀ imm 71 ; 1 ♀ juv 65·5. *Wing* 4 ♂ ad 146·5–152 (148·6) ; 4 ♀ ad 139–143 (141·2) ; 1 ♀ imm 138 ; 1 ♀ juv 135. *Tail* (outer rectrices) 4 ♂ ad 129–135 (131·1) ; 3 ♀ ad 120–127·5 (124·8); 1 ♀ imm 121·5; 1 ♀ juv 119. *Tail* (fork depth) 4 ♂ ad 7–10·5 (8·1) ; 3 ♀ ad 2·5–7 (4·7) ; 1 ♀ imm 6 ; 1 ♀ juv 0·5. *Bill* 4 ♂ ad 34–37 (36·0) ; 4 ♀ ad 32–34·5 (33·6) ; 1 ♀ imm 33 ; 1 ♀ juv 32·5.

Iris orange to orange-red ; imm red ; juv dull orange. *Bill* black. *Foot* black.

The " immatures " are doubtfully separated as birds in the second year plumage, on the basis of somewhat more rounded and less curled tails (see Vaurie, 1949 : 206).

(M. 121) ***Dicrurus hottentottus longirostris*** (Ramsay, 1882)

References. Vaurie, 1949 : 291. See Mayr & Vaurie, 1948.

Range. San Cristoval.

Specimens. San Cristoval : Goge 2 ♂ ad, 2 ♂ imm, 1 ? imm ; Nagasi 1 ♂ ad, 3 ♂ imm, 1 ? imm. 1 ♂ ad to OUM.

Weight 3 ♂ ad 85·5–96·5 (91·5) ; 5 ♂ imm 78·5–89·5 (83·4). *Wing* 3 ♂ ad 144–152 (149·3); 5 ♂ imm 137–145 (140·1). *Tail* (outer rectrices) 2 ♂ ad 130, 140; 3 ♂ imm 120·5–128 (124·2). *Tail* (fork depth) 2 ♂ ad 7, 15 ; 3 ♂ imm 2–4·5 (3·0). *Bill* 3 ♂ ad 44–46 (44·8) ; 5 ♂ imm 39–44 (41·8).

Iris deep dull red to deep red-brown ; imm dark brown to dark greyish brown. *Bill* black ; 1 imm with pale horn tip. *Foot* black.

The immature specimens are separated on their more rounded and less curled rectrices. They average less glossy above, and smaller, and must be in their second-year plumage (see Vaurie, 1949 : 206).

Notes. The two races in the Solomons span virtually the whole range of variation shown by the highly polytypic *D. hottentottus*, in bill-form and the development of rictal bristles. One might expect a greater difference in diet than Cain & Galbraith's (1956) small samples showed. With its very long compressed bill and weak bristles, *longirostris* seems the better adapted to a diet of lizards and large insects.

(M. 123) ***Corvus woodfordi woodfordi*** (Ogilvie-Grant, 1887)

References. Vaurie, 1958 : 9.

Range. Choiseul, Ysabel, Guadalcanal—irregular geographical variation in size.

Specimens. Guadalcanal : Betilonga 1 ♂ ad, 3 ♀ ad. 1 ♀ ad to OUM.

Weight 1 ♂ ad 425 ; 3 ♀ ad 375–405 (386·0). *Wing* 2 ♀ ad 262, 265. *Tail* 1 ♂ ad 130 ; 3 ♀ ad 118–126 (123·0). *Bill* 1 ♂ ad 64 ; 3 ♀ ad 60·5–61 (60·8).

Iris grey. *Skin* of throat purplish red. *Bill* ivory, shading to pale blue and purple basally, tip black. *Foot* black.

Notes. We follow Vaurie (1958) in regarding the black-billed *meeki* of Bougainville as conspecific with *woodfordi*, and the population of larger birds on Ysabel (*vegetus*) as belonging subspecifically to the latter.

(H) *Gymnorhina tibicen* subspecies

References. Condon, 1951 : 67 ; Amadon, 1951 : 20. See Amadon, 1953.

Range. Southern and eastern Australia, introduced to Guadalcanal.

Notes. Records for Guadalcanal are all from the grasslands near the Tenaru River (Beecher, 1945 : 36 ; Baker, 1948 : 17 ; Cain & Galbraith, 1956 : 288), where the species is probably not well-established.

(M. 124) ***Nectarinia jugularis flavigaster*** Gould, 1843

References. Rothschild & Hartert, 1914 : 297 ; Mayr & Rand, 1937 : 210. See Delacour, 1944.

Range. Admiraltys, Bismarcks, Solomons except San Cristoval and Santa Ana (coasts).

Specimens. Guadalcanal : Tenaru 8 ♂ ad, 1 ♂ juv, 6 ♀ ad, 1 ♀ juv, 2 ? ad. Ugi 2 ♀ ad. 1 ♂ ad to OUM.

Weight 8 ♂ ad 9·5–11 (10·2) ; 1 ♂ juv 9 ; 8 ♀ ad 8·5–9·5 (8·9) ; 1 ♀ juv 8. *Wing* 7 ♂ ad 54–58·5 (56·0) ; 1 ♂ juv 53 ; 8 ♀ ad 48·5–53 (51·9) ; 1 ♀ juv 47·5. *Tail* 7 ♂ ad 34·5–38·5 (37·0) ; 1 ♂ juv 31·5 ; 7 ♀ ad 31·5–35 (33·9) ; 1 ♀ juv 29·5. *Bill* 6 ♂ ad 22–24 (23·2) ; 1 ♂ juv 21 ; 8 ♀ ad 21–22 (21·6) ; 1 ♀ juv 21·5.

Iris dark to very dark brown. *Bill* black ; 1 juv base of mandible blackish horn, gape yellow. *Foot* black, shanks sometimes fuscous ; 1 juv leaden-black.

The juveniles are distinguished from adult females by laxer plumage, paler carotenoid, and lack of blackish subterminal patches on the dorsal feathers.

Notes. This widely-distributed species has not been recorded from San Cristoval (see Mayr, 1945*a* : 279), and there are no specimens from there in the AMNH (Amadon, *in litt.*) or BM(NH). The expedition did not encounter it at Manewiriwiri, where natives did not recognize a coloured figure (Mayr, 1945*a* pl. 3, figs. 34–35). French (*in litt.*) doubts its presence on the island. Nor is it found on Santa Ana, though present on Ugi (see Cain & Galbraith, 1956 : 104) and the Three Sisters (Cain & Galbraith, 1956 ; French, 1957). Its absence from San Cristoval may be related to the presence of two species of *Myzomela*, ecologically very similar to *Nectarinia* and both abundant along the coast. Ripley (1959) discusses competition between these two genera in the Moluccas, while Salomonsen (personal communication) finds a similar geographical relationship in the Bismarcks (see Ripley, 1961). That *N. jugularis* and *M. nigrita* have precisely complementary ranges may be fortuitous : *M. cardinalis*, which coexists with the former on Ugi and the Three Sisters, might be expected, as another wholly coastal species, to compete with it the more intensely.

(M. 125) ***Myzomela cardinalis pulcherrima*** Ramsay, 1881

REFERENCE. Mayr, 1932*a* : 24. See Koopman, 1957.

RANGE. San Cristoval, Ugi, Three Sisters (coasts).

SPECIMENS. San Cristoval : Manewiriwiri 6 ♂ ad, 12 ♂ imm, 2 ♂ juv, 6 ♀ ad, 3 ♀ imm, 1 ♀ juv, 1 ? imm, 3 ? juv. Ugi 33 ♂ ad, 13 ♂ imm, 3 ♂ juv, 7 ♀ ad, 4 ♀ imm, 1 ? imm, 1 ? juv. 1 ♂ imm, 1 ♂ juv, 1 ♀ ad, 1 ♀ imm, 1 ? juv to AMNH ; 1 ♂ ad, 1 ♂ imm, 1 ♀ ad to OUM.

Weight San Cristoval 6 ♂ ad 14·5–16 (15·4) ; 12 ♂ imm 14–16 (15·0) ; 2 ♂ juv 12·5, 15·5 ; 6 ♀ ad 11·5–13 (12·3) ; 3 ♀ imm 11·5–13·5 (12·5) ; 1 ♀ juv 13·5 ; Ugi 33 ♂ ad 14–18 (15·8) ; 13 ♂ imm 13·5–17·5 (15·5) ; 3 ♂ juv 14·5–16 (15·3) ; 7 ♀ ad 12–14 (13·0) ; 4 ♀ imm 12–13·5 (12·7). *Wing* San Cristoval 5 ♂ ad 68–74 (70·6) ; 12 ♂ imm 65·5–70·5 (67·9) ; 1 ♂ juv 66 ; 5 ♀ ad 61·5–65 (63·8) ; 3 ♀ imm 60–64 (62·0) ; 1 ♀ juv 61·5 ; Ugi 28 ♂ ad 67–74 (69·7) ; 11 ♂ imm 65–68·5 (67·2) ; 3 ♂ juv 66–69·5 (67·5) ; 6 ♀ ad 61–66 (63·3) ; 3 ♀ imm 61–63 (61·8). *Tail* San Cristoval 4 ♂ ad 46–47·5 (46·7) ; 10 ♂ imm 38·5–44·5 (41·5) ; 1 ♂ juv 40·5 ; 5 ♀ ad 39–41·5 (40·0) ; 3 ♀ imm 39–40 (39·7) ; 1 ♀ juv 37·5 ; Ugi 22 ♂ ad 42–48 (44·9) ; 13 ♂ imm 39–44 (41·6) ; 3 ♂ juv 40–43 (41·3) ; 3 ♀ ad 38·5–40 (39·3) ; 3 ♀ imm 37–38·5 (37·7). *Bill* San Cristoval ; 6 ♂ ad 20·5–22 (21·0) ; 11 ♂ imm 19·5–21 (20·1) 2 ♂ juv 16·5, 19·5 ; 5 ♀ ad 18·5–20 (19·3) ; 3 ♀ imm 19–19·5 (19·3) ; 1 ♀ juv 18 ; Ugi 29 ♂ ad 20–22 (20·8) ; 10 ♂ imm 19–21·5 (20·3) ; 3 ♂ juv 20–21 (20·3) ; 6 ♀ ad 19–19·5 (19·3) ; 3 ♀ imm 19–19·5 (19·2).

Iris very dark brown. *Bill* black, ♂ gape occasionally fuscous or yellowish fuscous, ♀ base of mandible sometimes brownish and gape yellowish (dark horn to golden-yellow) ; imm and juv base of mandible horn, gape fuscous-yellow to golden-yellow, base of ♀ maxilla greyish horn, ♂ sometimes greyish. *Foot* dark grey, toes darker and browner, shanks bluish (often patchily) with silvery sheen, ♂ ad average darkest.

The adult males are readily separable and do not show much colour variation, but the other plumages are similar, intergrading and variable. The colour and texture of wing and tail are much affected by wear, and there is little difference between those of juveniles, immatures and adult females. The red pigmentation is very variable in extent, and in whether it forms a general wash or (as in the adult males) is confined to specialized feather-tips lacking barbules.

Adult females are dorsally like immature males, and differ ventrally in having the red virtually restricted to throat and breast, with the belly usually sombre grey scarcely washed with pink, olivaceous or buff. Immature females differ from adults in having red tips only on the back ; red on the head confined to the forehead and front of the crown ; the back averaging paler and more olivaceous or brownish, with much less red ; the ventral red much less intense, but extending further posteriorly ; and the belly paler and more decidedly washed with red or olive. Immature males differ from immature females in having much more red ventrally, with specialized red tips. The brownish hind-crown and nape of a few immature males, resembling those of immature females, probably belong to the juvenile plumage. There is scarcely any overlap, in either sex, in the gonadial development of the adult and immature series.

Juveniles are very like immatures, in both texture and coloration of plumage. Their identification as such depends on one male BM(NH) reg. no. 1959.21.1374) which is coloured much like immatures, as far as can be determined from its somewhat disarranged plumage, yet is clearly very young : its bill is small (16·5 mm), wing and tail growing (52·5 and 20·5 mm), and contour-plumage scanty with large naked tracts. The plumage considered to be juvenile has the hind-crown and nape dull brown with a faint reddish wash, instead of bright red as in immatures, and is much less intense red beneath. Female and unsexed juveniles are like immature females, but with less red on the crown.

NOTES. Most of the populations attributed to this species (Mayr, 1932 ; Koopman, 1957) are rather uniform in basic colour-pattern, though variable in dimensions, intensity of pigmentation, and degree of sexual dimorphism. However, the form on Rotuma (*chermesina* Gray) is very different, and perhaps belongs to the *lafargei* superspecies. It resembles *M. malaitae* of that group rather than the races of *M. cardinalis*. The presence of a putative member of the superspecies (*M. jugularis*) in Fiji demonstrates its colonizing potential.

(M. 126) ***Myzomela melanocephala*** (Ramsay, 1879)

REFERENCES. Mayr, 1932*a* : 26. See Koopman, 1957.

RANGE. Guadalcanal, Savo, Florida Is.

SPECIMENS. Guadalcanal : Tenaru 2 ♂ ad, 2 ♂ juv ; Betilonga 9 ♂ ad, 1 ♂ imm, 4 ♀ ad, 1 ? juv ; Turipava 1 ♂ ad, 1 ♂ imm, 1 ♂ juv, 1 ♀ ad, 1 ? imm, 1 ? juv. 1 ♂ ad, 1 ♀ ad, 1 ? imm to OUM.

Weight 12 ♂ ad 11–14 (12·8) ; 5 ♂ imm 12–15 (13·6) ; 3 ♀ juv 10–12·5 (11·3) ; 5 ♀ ad 10–12·5 (11·2). *Wing* 11 ♂ ad 63–68·5 (65·6) ; 2 ♂ imm 64, 65 ; 2 ♂ juv 62, 63·5 ; 4 ♀ ad 57–60 (58·7). *Tail* 8 ♂ ad 44–46 (44·8) ; 2 ♂ imm 43, 44 ; 3 ♂ juv 37·5–42 (40·2) ; 4 ♀ ad 38–40·5 (39·4). *Bill* 11 ♂ ad 20–23 (21·9) ; 2 ♂ imm 20·5, 22 ; 3 ♂ juv 19·5–20 (19·7) ; 5 ♀ ad 19·5–20·5 (20·2).

Iris dark brown. *Bill* black, ♀ gape sometimes dull yellow ; juv base (+ 1 tip) dull yellow, gape bright yellow. *Foot* grey, bluish or greenish to fuscous, soles yellowish.

The immature plumage is considerably laxer than the adult, especially where it is most ochraceous in colour (rump, belly, upper wing-coverts). The juvenile plumage is very similar, but somewhat laxer still, duller on nape and interscapulars, and with the black on the head still duller and more restricted.

(M. 127) ***Myzomela tristrami*** Ramsay, 1882

REFERENCES. Mayr, 1932*a* : 29. See Koopman, 1957.

RANGE. San Cristoval, Santa Ana.

SPECIMENS. San Cristoval : Manewiriwiri 5 ♂ ad, 1 ♂ imm, 5 ♀ ad, 2 ? imm ; Goge 12 ♂ ad, 4 ♂ imm, 5 ♀ ad, 1 ? juv ; Nagasi 4 ♂ ad, 3 ♂ imm, 1 ♀ juv, 1 ? imm. 1 ♂ ad, 1 ♂ imm, 1 ♀ ad to OUM.

Weight 21 ♂ ad 12·5–16·5 (14·4) ; 8 ♂ imm 12·5–15·5 (14·1) ; 10 ♀ ad 11·5–13 (12·3) ; 1 ♀ juv 11·5. *Wing* 18 ♂ ad 66–69·5 (67·5) ; 8 ♂ imm 64–67 (65·7) ; 8 ♀ ad 61·5–64·5 (62·9) ; 1 ♀ juv 60. *Tail* 19 ♂ ad 40–46 (44·2) ; 8 ♂ imm 39–43 (41·6) ; 7 ♀ ad 40–42·5 (41·1) ; 1 ♀ juv 38. *Bill* 18 ♂ ad 21–23·5 (22·0) ; 5 ♂ imm 21–24 (22·1) ; 8 ♀ ad 18–20·5 (19·7) ; 1 ♀ juv 19.

Iris very dark brown. *Bill* black ; imm and juv basal 2/3 yellow, greyish above, gape brighter. *Foot* black or dark slate, sometimes bluish, ♂ ad average darkest.

What appears to be the juvenile plumage is somewhat softer than the immature, and less blackish below, but not markedly more olivaceous (cf. Mayr, 1932*a*).

NOTES. It seems unwise to associate this form with *M. nigrita* of the New Guinea region (Stresemann, 1923 : 51 ; Mayr, 1932*a* ; Koopman, 1957) on the single all-obscuring character of total melanism. It may rather be a member of the *lafargei* superspecies ; especially since its nearest neighbour, *M. melanocephala*, also lacks red and shows little sexual dimorphism. The fact that two specimens (from Sant Ana—Mayr, 1932*a*) have red on the rump (like *M. eichhorni* and *M. malaitae*), and not on the forehead and throat (as in the females of many races of *M. nigrita*) nor the crown (as in the male of *M. n. forbesi*), supports this conclusion, as does intensive study by Salomonsen (personal communication).

Ramsay's (1882*c* : 27) record for Ugi refers only to Morton's account, unsupported by specimens. The species has not since been found there (Mayr, 1932 ; Cain & Galbraith, 1956), and is not to be expected on a small island in company with both *M. cardinalis* and *Nectarinia jugularis*.

(M. 129) ***Meliphaga inexpectata*** (Hartert, 1929)

REFERENCES. Hartert, 1929 : 8 ; Mayr, 1932*a* : 13.

RANGE. Guadalcanal (mountains).

SPECIMENS. Guadalcanal : Turipava 6 ♂ ad, 1 ♂ imm, 10 ♀ ad, 3 ♀ imm. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 6 ♂ ad 41·5–48·5 (46·8) ; 1 ♂ imm 40 ; 10 ♀ ad 37·5–44·5 (40·1) ; 3 ♀ imm 33·5–34 (33·8). *Wing* 5 ♂ ad 109·5–115 (112·9) ; 1 ♂ imm 104 ; 10 ♀ ad 96–102·5 (100·0) ; 3 ♀ imm 95–97·5 (95·2). *Tail* 4 ♂ ad 95–96 (95·4) ; 1 ♂ imm 91·5 ; 7 ♀ ad 76–86 (82·8) ; 3 ♀ imm 79–80·5 (79·7). *Bill* 4 ♂ ad 31·5–35 (32·9) ; 1 ♂ imm 32 ; 8 ♀ ad 28–31 (29·6) ; 3 ♀ imm 26·5–31 (28·2).

Iris brown, light to dark (once " black "), sometimes reddish ; imm dark grey-brown. *Bill* black. *Foot* blue-grey, sometimes pale or silvery, claws fuscous ; imm shanks fuscous-tinged.

The rectrices of the adult females are narrower than those of adult males, but not as soft and pointed as those of immatures.

NOTES. We follow the generic assignment of Salomonsen (*in litt.*), who places " *Meliphaga* " *bougainvillei* of the Bougainville mountains in *Melilestes*. With the discovery of a new genus and species in the mountains of New Britain (Gilliard, 1960*a*), the distribution of large honeyeaters in Northern Melanesia (except for the *Philemon moluccensis* superspecies) becomes even more puzzling : *Vosea whitemanensis* in the mountains of New Britain, *Melilestes bougainvillei* in the mountains of Bougainville, *Meliphaga inexpectata* in the mountains of Guadalcanal, and *Meliarchus sclateri* on San Cristoval.

(M. 130) **Meliarchis sclateri** (Gray, 1870)

REFERENCES. *Cat. Birds B.M.* 9 : 279 ; Mayr, 1932*a* : 12.

RANGE. San Cristoval.

SPECIMENS. San Cristoval : Goge 13 ♂ ad, 1 ♂ imm, 4 ♀ ad, 2 ♀ juv ; Nagasi 2 ♂ ad, 2 ♂ imm, 5 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 14 ♂ ad 75·5–88 (80·2) ; 3 ♂ imm 68–77 (72·5) ; 9 ♀ ad 51·5–58·5 (55·6) ; 1 ♀ juv 45. *Wing* 4 ♂ ad 122–136 (129·5) ; 3 ♂ imm 121–123·5 (122·5) ; 6 ♀ ad 107–115 (111·1). *Tail* 7 ♂ ad 104·5–110·5 (108·5) ; 3 ♂ imm 99–102·5 (100·5) ; 7 ♀ ad 87–97 (93·1). *Bill* 12 ♂ ad 39–42 (40·5) ; 3 ♂ imm 39·5–41 (40·2) ; 8 ♀ ad 34·5–36·5 (35·4) ; 2 ♀ juv 30, 30.

Iris pale greenish grey or brown, dark brown centrally ; juv dark brown. *Skin* round eye pale blue-grey, eyelid whitish tinged with yellow, greenish or fuscous. *Bill* silvery greenish or straw distally, shading to silvery blue-grey basally, gape whitish with yellow inner surface ; imm and juv more or less streaked with black. *Foot* pale blue-grey, shank sometimes yellow-washed.

Besides the characters noted by Mayr (1932*a*), immatures differ from adults in lacking bristly black shafts in the throat plumage, lacking the blackish subterminal patches which give a scaled effect to the mid-back, and having the back browner and the rump more rufous. The juveniles differ from immatures in having softer plumage, especially ventrally and on the crown and nape, the centres of the dorsal feathers less blackish and their edges less yellowish, and the ventral shaft-streaking still less distinct.

(J) *Myzantha melanocephala* subspecies

RANGE. Eastern and southeastern Australia and Tasmania ; introduced to Three Sisters (French, 1957).

(M. 132) **Zosterops ugiensis oblita** Hartert, 1929

REFERENCES. Mees, 1961 : 162.

RANGE. Guadalcanal.

SPECIMENS. Guadalcanal : Betilonga 15 ♂ ad, 1 ♂ juv, 9 ♀ ad, 1 ? ad, 2 ? juv ; Turipava 6 ♂ ad, 4 ♀ ad. 1 ♂ ad to OUM.

Weight Betilonga 16 ♂ ad 13·5–16·5 (14·9) ; 1 ♂ juv 14·5 ; 9 ♀ ad 15–17 (16·4) ; Turipava 6 ♂ ad 13–16 (15·1) ; 4 ♀ ad 13·5–18 (15·6). *Wing* Betilonga 15 ♂ ad 64–69 (66·0) ; 8 ♀ ad 63·5–69 (65·4) ; Turipava 5 ♂ ad 66–70·5 (68·3) ; 4 ♀ ad 62–66 (64·0). *Tail* Betilonga 14 ♂ ad 44·5–48·5 (46·5) ; 7 ♀ ad 44–47 (45·4) ; Turipava 5 ♂ ad 46·5–49 (48·1) ; 3 ♀ ad 44–46 (44·8). *Bill* Betilonga 13 ♂ ad 15–16·5 (16·1) ; 1 ♂ juv 14·5 ; 8 ♀ ad 15–16·5 (16·1) ; Turipava 5 ♂ ad 15·5–16·5 (16·1) ; 3 ♀ ad 16–16·5 (16·2).

Iris light brown ; juv grey-brown to light brown. *Skin* round eye dark grey. *Bill* black, base of mandible whitish ; juv maxilla blackish streaked with pale horn, mandible whitish or pale horn streaked with blackish, gape flesh. *Foot* bluish grey, often with yellowish or fuscous tinge.

The juveniles differ from adults in having softer plumage, more narrowly-pointed rectrices, and primaries with less falcation, and in more dilute carotenoids (under tail-coverts paler yellow, olive duller and more citrine especially on outer edges of remiges), olive edges continued to the tips of rectrices, and lower cheeks without grey wash.

NOTES. The geographical and altitudinal distribution of species of *Zosterops* in the Solomons is puzzling (despite Cain, 1956*b* : 13).

(M. 132) ***Zosterops ugiensis ugiensis*** (Ramsay, 1882)

REFERENCES. Mees, 1961 : 158 (*rendovae*).

RANGE. San Cristoval.

SPECIMENS. San Cristoval : Nagasi 5 ♂ ad, 1 ♂ juv, 4 ♀ ad. 1 ♂ ad to OUM.

Weight 5 ♂ ad 18·5–19·5 (18·9) ; 1 ♂ juv 17 ; 4 ♀ ad 17·5–21·5 (19·5). *Wing* 5 ♂ ad 68–70 (69·1) ; 1 ♂ juv 64 ; 4 ♀ ad 66–68 (66·6). *Tail* 5 ♂ ad 43–45·5 (44·5) ; 4 ♀ ad 40·5–44 (42·3). *Bill* 5 ♂ ad 16·5–18 (17·3) ; 1 ♂ juv 17 ; 4 ♀ ad 16·5–18 (17·1).

Iris light brown. *Bill* black, extreme base of mandible dull fuscous to ivory ; juv base of mandible grey. *Foot* bluish to greenish or fuscous grey, sometimes patchy, toes average darker and bluer.

The plumage of the juvenile is slightly softer than that of adults, but much firmer than that of juvenile *oblita*, and it has growing rectrices of adult shape. It differs in colour from adults in having the brownish wash on the forehead (very variable in intensity between adults) much reduced though discernible, and the dorsal olive duller and more citrine.

NOTES. Mees (1955 ; 1961 : 160–162) has pointed out that the name *rendovae*, which had always been applied to the quite different *Zosterops* on Rendova, is the valid name for the present species under the International Rules. Arguments put forward to disprove this (Galbraith, 1957) are incorrect (China *in litt.* I.C.Z.N. ref. Z.N.(S)1223). While the other objections to the change are largely irrelevant, the cardinal point remains : transfer of a name in use for one taxon to another is highly undesirable, because of the confusion it is likely to cause, in a way that simple adoption of an unfamiliar synonym is not. It is quite untrue that name-transfer in the present case would affect only museum workers (Mees, 1961), even if we accept a pessimistic view of future field work in the Solomons. The name *Zosterops rendovae* has been repeatedly used for the polytypic species or superspecies in the New Georgia Group, in widely-read works on evolution (e.g. Mayr, 1942; Lack, 1947; Cain, 1954*a*).

In order to avoid this transfer, I. C. J. G. will apply to the International Commission for the suppression of the name *rendovae* under the plenary powers, an action approved by Mees (1961). Use of the name *rendovae* in either sense would now be objectionable, and in order to avoid confusion a favourable decision by the Commission is here anticipated. Mees (1961 : 143–151) should be followed for the nomenclature of the New Georgia Group superspecies, and Mayr (1945*a*) for that of the present species and race.

(M. 136) ***Dicaeum aeneum becki*** Hartert, 1929

REFERENCES. Mayr, 1955 : 39; Salomonsen, 1960 : 33. See Mayr & Amadon, 1947.

RANGE. Guadalcanal.

SPECIMENS. Guadalcanal: Betilonga 19 ♂ ad, 5 ♂ imm, 10 ♀ ad, 1 ? imm; Nala 1 ♀ ad; Turipava 1 ♂ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 22 ♂ ad 8·5–10·5 (9·6); 5 ♂ imm 9·0–10·5 (9·5); 9 ♀ ad 8–9·5 (8·6). *Wing* 20 ♂ ad 50·5–56·5 (52·9); 5 ♂ imm 50·5–54 (52·4); 8 ♀ ad 49–53 (49·9). *Tail* 15 ♂ ad 26–29 (27·2); 3 ♂ imm 25–26 (25·5); 5 ♀ ad 23·5–26 (24·8). *Bill* 14 ♂ ad 12–13·5 (12·5); 5 ♂ imm 11·5–12·5 (12·2); 7 ♀ ad 11·5–12·5 (12·2).

Iris dark brown, 1 ♂ ad light brown, 3 ♀ ad dark grey-brown. *Bill* black, ♂ base of mandible often grey to whitish, ♀ bill sometimes greyish or fuscous, and more or less of mandible always whitish; imm gape and more or less of mandible orange. *Foot* dark grey to black, often fuscous, sometimes bluish.

The females have a more or less conspicuous hoary loral spot, and (where the orbital area is well-preserved) a narrow white circlet round the eye reminiscent of *Zosterops* species. Neither character is shown by any male (except that an adult sexed as a male with unenlarged testes, and two unsexed adults, agree with the females in all characters, and have been included with them).

The plumage of the immatures is somewhat scantier on flanks and rump than that of adults, but not otherwise different in texture or the shape of remiges or rectrices. The immature female is distinguished from adult females only by its orange-based bill; while immature males also have less red on the breast, more white on the lower throat, the grey of the lower breast paler and more olivaceous, the olive of the flanks duller, and the dorsal green gloss somewhat duller and bluer and more sharply restricted to the feather-tips.

NOTES. The population on Malaita is a distinct race, *D. a. malaitae* Salomonsen (1960 : 34), not simply intermediate between *aeneum* and *becki* (cf. Mayr, 1955).

(M. 137) ***Dicaeum tristrami*** Sharpe, 1883

REFERENCES. Sharpe, 1883 : 579; Rothschild & Hartert, 1908*b* : 364. See Mayr & Amadon, 1947; Salomonsen, 1960.

RANGE. San Cristoval.

Specimens. San Cristoval: Manewiriwiri 1 ♀ ad; Goge 10 ♂ ad, 1 ♂ imm, 4 ♀ ad, 2 ♀ imm; Nagasi 4 ♂ ad, 3 ♀ ad. 1 ♂ ad, 1 ♀ ad to OUM.

Weight 14 ♂ ad 11–13 (11·9); 1 ♂ imm 11; 8 ♀ ad 10–12·5 (11·4); 2 ♀ imm 10·5, 11. *Wing* 12 ♂ ad 56·5–60·5 (58·9); 1 ♂ imm 56·5; 8 ♀ ad 54·5–57·5 (55·9); 2 ♀ imm 55·5, 56·5. *Tail* 7 ♂ ad 27–30 (28·8); 1 ♂ imm 27; 6 ♀ ad 25·5–28·5 (27·3); 2 ♀ imm 26·5, 28. *Bill* 12 ♂ ad 12·5–13·5 (13·1); 1 ♂ imm 13; 8 ♀ ad 11·5–13 (12·5); 2 ♀ imm 12, 12·5.

Iris very dark brown. *Bill* black; imm pale in dried skin, gape and more or less of mandible dull orange-yellow or pale yellow. *Foot* black to dull slate, often brownish or bluish especially on shanks.

The sexes are not quite alike, but differ in the distribution of white on the head (Rothschild & Hartert, 1908*b*; despite Mayr & Amadon, 1947; Salomonsen, 1960 : 35). Males have a white area behind and below the auriculars (which it may invade to some extent), no white on the chin and upper throat, but whitish scaling on the lower throat and breast. Females have the auriculars themselves and the chin and upper throat white, while the brown breast-shield is unscaled but smaller.

The immatures have sparsely-feathered chins and distinctly softer plumage than adults, and might be thought much younger than those of *D. aeneum becki*. However, they do not agree with Rothschild & Hartert's (1908*b*) description, which may refer to juveniles. They differ in pattern from adults in being more uniform, without the sharp contrast between dark crown and pale mantle, with the white edges on the head confined to the forehead, with the breast-shield paler and greyer and less sharply distinct from the whitish underparts, and (in the female) with little white on the throat.

Notes. It must be emphasized that this species can be associated with the superspecies to which *D. aeneum* belongs (by Mayr & Amadon, 1947 : 21; Mayr, 1955 : 39) solely on the geographical grounds that only the *erythrothorax-hirundinaceum* complex occurs in the Australo-Papuan area. Apart from its large size, heavy bill and total lack of carotenoids, *D. tristrami* shows a pattern of melanin distribution unique in the family, though somewhat reminiscent of certain western *Dicaeum* (e.g. *D. rectrocinctum*) and even of *Oreocharis arfaki*. It seems best to regard it as a relict species of unknown affinities, which by competition excludes *D. aeneum* from San Cristoval (cf. Salomonsen, 1960 : 17). It cannot be associated with any particular species; certainly not with *D. eximium* merely because both are somewhat phaeomelanic.

(M. 138) **Erythrura trichroa woodfordi** Hartert, 1900

References. Mayr, 1931*d* : 5. See Delacour, 1943.

Range. Guadalcanal.

Specimens. Guadalcanal: Betilonga 1 ♂ ad, 1 ♀ imm.

Weight 1 ♂ ad 15·5; 1 ♀ imm 16. *Wing* 1 ♀ imm 61. *Tail* 1 ♀ imm 35. *Bill* 1 ♂ ad 15, 1 ♀ imm 14.

Iris dark brown. *Bill* black; imm base of mandible whitish. *Foot* flesh, fuscous-washed; imm pale straw.

Both specimens are rather dark green dorsally.

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REFERENCES

The typography of titles is made uniform throughout, and the collective title " Birds collected during the Whitney South Sea Expedition, no.— " is abbreviated to " Whitney,— ". Issue numbers are given in parentheses, where each comprises a single paper or group of related papers.

ALEXANDER, W. B. 1954. *Birds of the Ocean. A handbook for voyagers.* 2nd ed. London & New York ; Putnam : xiv + 306 pp.

AMADON, D. 1941. Notes on some Australian birds of prey. *Emu*, **40** : 365–384.

—— 1942*a*. Whitney, 49. Notes on some non-passerine genera, 1. *Amer. Mus. Novit.* (1175) : 1–11.

—— 1942*b*. Whitney, 50. Notes on some non-passerine genera, 2. *Amer. Mus. Novit.* (1176) : 1–21.

—— 1943*a*. Whitney, 52. Notes on some non-passerine genera, 3. *Amer. Mus. Novit.* (1237) : 1–22.

—— 1943*b*. The genera of starlings and their relationships. *Amer. Mus. Novit.* (1247) : 1–16.

—— 1949. The seventy-five per cent rule for subspecies. *Condor* **51** : 250–258.

—— 1951. Taxonomic notes on the Australian butcher-birds (family Cracticidae). *Amer. Mus. Novit.* (1504) : 1–33.

—— 1953. Further remarks on the Cracticidae. *S. Aust. Orn.* **21** : 6–7.

—— 1956. Remarks on the starlings, family Sturnidae. *Amer. Mus. Novit.* (1803) : 1–41.

—— & WOOLFENDEN, G. 1952. Notes on the Mathews' collection of Australian birds. The order Ciconiiformes. *Amer. Mus. Novit* (1564) : 1–16.

ANON. 1952. Pelicans blown into the Solomons. *Pacific Islands Monthly*, **23** (2) : 78. Sydney. [*n.v.*]

AUBER, L. 1938. Die Rassen- und Artenkreise des Genus *Eos* Wagler (Aves). Ein taxonomisch-phylogenetische Studie. *Festschrift zum* 60. *Geburstage von Professor Dr. Embrik Strand.* **4** : 673–782. Riga ; Latvija.

—— 1957. The distribution of structural colours and unusual pigments in the class Aves. *Ibis*, **99** : 463–476.

AUSTRALIA 1950–1951. *The resources of the Territory of Papua and New Guinea.* Canberra ; Dept. Nat. Devel., **1** : 150 pp. + corrigenda ; **2** : 9 maps + vi pp.

B.H.I. 1942. *Carte générale bathymétrique des océans.* 3rd ed. Sheet A$_{\text{III}}$. Monte-Carlo ; Bureau Hydrographique International.

BAKER, E. C. S. 1926. *The fauna of British India. Birds,* **3** London ; Taylor & Francis : xx + 489 pp.

BAKER, R. H. 1948. Report on collections of birds made by United States Naval Medical Research Unit No. 2 in the Pacific war area. *Smithson. misc. Coll.* **107** (15) : 1–74.

BEECHER, W. J. 1945. A bird collection from the Solomon Islands. *Fieldiana, Zool.* **31** (4) : 31–37.

BEMMEL, A. C. V. VAN. 1948. A faunal list of the birds of the Moluccan Islands. *Treubia,* **19** : 323–402.

BERGER, A. J. 1955. On the anatomy and relationships of glossy cuckoos of the genera *Chrysococcyx, Lampromorpha,* and *Chalcites. Proc. U.S. nat. Mus.* **103** : 585–597.

BOCK, W. J. 1956. A generic review of the family Ardeidae (Aves). *Amer. Mus. Novit.* (1799) : 1–49.

BOGERT, C. 1937. Whitney, 34. The distribution and the migration of the Long-tailed Cuckoo (*Urodynamis taitensis* Sparrman). *Amer. Mus. Novit.* (933) : 1–12.

BRADLEY, D. 1957. Birds of the Solomon Islands. *Ibis,* **99** : 352–353.

—— 1962. Additional records of birds from Rennell and Bellona Islands. *The Natural History of Rennell Island, British Solomon Islands,* **4** (32) : 11–12. Copenhagen ; Danish Science Press ; ed. Wolff.

—— & WOLFF, T. 1956. The birds of Rennell Island. *The natural history of Rennell Island, British Solomon Islands,* **1** (7) : 85–120. Copenhagen ; Danish Science Press ; ed. Wolff.

BRAESTRUP, F. W. 1956. The significance of the strong "oceanic" affinities of the vertebrate fauna on Rennell Island. *The natural history of Rennell Island, British Solomon Islands,* **1** (9) : 135–148. Copenhagen ; Danish Science Press ; ed. Wolff.

BULL, P. C. 1948. Field notes on waders in the south-west Pacific with special reference to the Russell Islands. *Emu,* **47** : 165–176.

CAIN, A. J. 1954*a*. *Animal species and their evolution.* London ; Hutchinson : 190 pp.

—— 1954*b*. Subdivisions of the genus *Ptilinopus* (Aves, Columbae). *Bull. Brit. Mus.* (*nat. Hist.*) *Zool.* **2** (8) : 265–284.

—— 1954*c*. Affinities of the fruit-pigeon *Ptilinopus perousii* Peale. *Ibis,* **96** : 104–110.

—— 1955. A revision of *Trichoglossus haematodus* and of the Australian platycercine parrots. *Ibis,* **97** : 432–479.

—— 1956*a*. The genus in evolutionary taxonomy. *Syst. Zool.* **5** : 97–109.

—— 1956*b*. Classification. *The ornithologists' guide :* 10–14. London ; Brit. Orn. Union ; ed. Hutson.

—— 1957. Range-changes and differential selection in fruit-pigeons of the *Ptilinopus purpuratus* species group. *Proc. Pacific Sci. Congr.* (8) **3A** : 1393–1412. Quezon ; Nat. Res. Council Philippines.

—— & GALBRAITH, I. C. J. 1955. Five new subspecies from the mountains of Guadalcanal (British Solomon Islands). *Bull. Brit. Orn. Cl.* **75** : 90–93.

—— —— 1956. Field notes on birds of the eastern Solomon Islands. *Ibis,* **98** : 100–134, 262–295.

—— —— 1957. [Birds of the Solomon Islands]. *Ibis,* **99** : 128–130.

CONDON, H. T. 1951. Notes on the birds of South Australia : occurrence, distribution and taxonomy. *S. Aust. Orn.* **20** : 26–68.

—— & AMADON, D. 1954. Taxonomic notes on Australian hawks. *Rec. S. Aust. Mus.* **11** : 189–246.

D.C.S. 1955. *Sketch map Guadalcanal* (*British Solomon Islands Protectorate*) 1 : 50,000. London ; Directorate of Colonial Surveys ; D.C.S. (Misc.) 91 : 14 sheets.

D.O.S. 1958. *British Solomon Islands San Cristoval sketch map* 1 : 50,000. London ; Directorate of Overseas Surveys ; D.O.S. 456 (Series 714) : 8 sheets.

DAHL, F. 1899. Das Leben der Vögel auf den Bismarckinseln nach eigenen Beobachtungen vergleichend dargestellt. *Mitt. zool. Mus. Berl.* **1** (3) : 107–222.

DANIS, V. 1938. Étude d'une nouvelle collection d'oiseaux de l'Ile Bougainville. *Bull. Mus. Hist. nat., Paris* (2) **10** : 43–47.

DAVIDSON, M. E. M. 1929. On a small collection of birds from Torres Strait islands, and from Guadalcanal Island, Solomon group. *Proc. Calif. Acad. Sci.* (4) **18** (10) : 245–260.

DAVIDSON, M. E. M. 1934. The Templeton Crocker Expedition to western Polynesian and Melanesian islands, 1933. No. 16. Notes on the birds. *Proc. Calif. Acad. Sci.* (4) **21** (16) : 189–198.

DELACOUR, J. 1943. A revision of the subfamily Estrildinae of the family Ploceidae. *Zoologica, N.Y.* **28** : 69–86.

—— 1944. Revision of the family Nectariniidae (sunbirds). *Zoologica, N.Y.* **29** : 17–38.

—— 1946. Notes on the taxonomy of the birds of Malaysia. *Zoologica, N.Y.* **31** : 1–8.

—— & MAYR, E. 1945. The family Anatidae. *Wilson Bull.* **57** : 3–55.

DONAGHHO, W. R. 1950. Observations on some birds of Guadalcanal and Tulagi. *Condor*, **52** : 127–132.

DORST, J. 1954. La Pélican à Lunettes aux Nouvelles-Hébrides. *Oiseau, Paris* (n.s.) **24** : 149–151.

FELL, H. B. 1947. The migration of the New Zealand Bronze Cuckoo *Chalcites lucidus lucidus* (Gmelin). *Trans. roy. Soc. N.Z.* **76** : 504–515.

FRENCH, W. 1957. Birds of the Solomon Islands. *Ibis*, **99** : 126–127.

FRITH, H. J. 1956. Breeding habits in the family Megapodiidae. *Ibis*, **98** : 620–640.

GALBRAITH, I. C. J. 1956. Variation, relationships and evolution in the *Pachycephala pectoralis* superspecies (Aves, Muscicapidae). *Bull. Brit. Mus. (nat. Hist.) Zool.* **4** (4) : 131–222.

—— 1957. On the application of the name *Zosterops rendovae* Tristram, 1882. *Bull. Brit. Orn. Cl.* **77** : 10–16.

GILLIARD, E. T. 1960*a*. Results of the 1958–1959 Gilliard New Britain Expedition. 1. A new genus of honeyeater (Aves). *Amer. Mus. Novit.* (2001) : 1–5.

—— 1960*b*. Results of the 1958–1959 Gilliard New Britain Expedition. 2. A new species of thicket warbler (Aves, *Cichlornis*) from New Britain. *Amer. Mus. Novit.* (2008) : 1–6.

GOODWIN, D. 1959. Taxonomy of the genus *Columba*. *Bull. Brit. Mus. (nat. Hist.) Zool.* **6** (1) : 1–23.

—— 1960. Taxonomy of the genus *Ducula*. *Ibis*, **102** : 526–535.

GRAY, G. R. 1873. Birds. In Brenchley, *Jottings during the cruise of H.M.S. Curacoa among the South Sea islands in* 1865 : 353–394. London ; Longmans, Green & Co.

GROVER, J. C. 1955. *Geology, mineral deposits and prospects of mining development in the British Solomon Islands Protectorate. Mem. interim geol. Surv. B.S.I.* (1). London ; Crown Agents : ix + 108 pp.

—— 1957. Some geographical aspects of the British Solomon Islands in the western Pacific. *Geogr. J.* **123** : 298–317.

—— 1958. *The Solomon Islands—geological exploration and research* 1953–1956. Chapters by Pudsey-Dawson, P. A. & Thompson, R. B. M. *Mem. geol. Surv. B.S.I.* (2). London ; Crown Agents : viii + 151 pp.

—— (ed.) 1960. *The British Solomon Islands geological record* 1957–1958. *Reports on investigations into the geology and mineral resources of the Protectorate.* London ; Crown Agents : v + 113 pp.

GURNEY, J. H. 1884. *A list of the diurnal birds of prey, with references and annotations ; also a record of specimens preserved in the Norfolk and Norwich Museum.* London ; van Voorst : xv + 187 pp.

HACHISUKA, M. 1931. Notes sur les oiseaux des Philippines. 1. Révision des colombes terrestres. *Oiseau, Paris* (n.s.) **1** : 23–29.

HAMLIN, H. 1931. Whitney, 14. Notes on the geography of Rennell Island and the ecology of its bird life. *Amer. Mus. Novit.* (488) : 1–6.

HARTERT, E. 1896. Contributions to the ornithology of the Papuan islands. 3. On the forms of *Macropteryx mystacea*. *Novit. Zool.* **3** : 19–20.

—— 1908. [Exhibition of birds from the Solomon Islands.] *Bull. Brit. Orn. Cl.* **21** : 105–107.

—— 1924*a*. The birds of New Hanover. *Novit. Zool.* **31** : 194–213.

—— 1924*b*. The birds of St. Matthias Island. *Novit. Zool.* **31** : 261–275.

—— 1926*a*. On the birds of Feni and Nissan Islands, east of South New Ireland. *Novit. Zool.* **33** : 33–48.

—— 1926*b*. On the birds of the district of Talasea in New Britain. *Novit. Zool.* **33** : 122–145.

HARTERT, E. 1929. Whitney, 8. Notes on birds from the Solomon Islands. *Amer. Mus. Novit.* (364) : 1–19.

HEINROTH, O. 1903. Ornithologische Ergebnisse der " I. Deutschen Südsee-Expedition von Br. Mencke " [concluded]. *J. Orn.* **51** : 65–125.

I.C.Z.N. 1956. Direction 43. *Opin. int. Comm. zool. Nom.* **1** (D.7.) : 171–210.

—— 1958. *Official list of specific names in zoology.* (1). London ; Int. Tr. Zool. Nomen ; ed. Hemming : xvi + 206 pp.

KEAST, A. 1957. Variation in the Australian kingfishers. (Aves : Alcedinidae). *Rec. Aust. Mus.* **24** (7) : 61–72.

—— 1958. Variation and speciation in the Australian Campephagidae (Passeres). *Aust. J. Zool.* **6** : 248–267.

KOOPMAN, K. F. 1957. Evolution in the genus *Myzomela* (Aves ; Meliphagidae). *Auk*, **74** : 49–72.

LACK, D. 1947. *Darwin's finches.* Cambridge ; C.U.P. : x + 208 pp.

LAIRD, M. 1954. Australian Pelicans in the Solomon Islands and New Hebrides. *Notornis*, **6** : 11–13.

MATHEWS, G. M. 1918. *The birds of Australia*, **7** (4) : 321–384. London ; Witherby.

—— 1927–1930. *Systema avium Australasianarum. A systematic list of the birds of the Australasian region.* London ; B.O.U. **1** : xvii + 426 pp.; **2** : iv + 427–1047 pp.

—— 1928. Bird notes. *Novit. Zool.* **34** : 372–373.

—— 1931. Additions and corrections to the " Systema avium Australasianarum ". *Ibis* (13) **1** : 44–57.

—— 1932. Additions and corrections to the " Systema avium Australasianarum ". 2. *Ibis* (13) **2** : 132–161.

—— 1933. Additions and corrections to the " Systema avium Australasianarum ". 3. *Ibis* (13) **3** : 87–97.

MAYR, E. 1931*a*. Whitney, 12. Notes on *Halcyon chloris* and some of its subspecies. *Amer. Mus. Novit.* (469) : 1–10.

—— 1931*b*. Whitney, 13. A systematic list of the birds of Rennell Island with descriptions of new species and subspecies. *Amer. Mus. Novit.* (486) : 1–29.

—— 1931*c*. Whitney, 14. The relationships and origin of the birds of Rennell Island. *Amer. Mus. Novit.* (488) : 7–11.

—— 1931*d*. Whitney, 15. The parrot finches (genus *Erythrura*). *Amer. Mus. Novit.* (489) : 1–10.

—— 1931*e*. Whitney, 16. Notes on fantails of the genus *Rhipidura*. *Amer. Mus. Novit.* (502) : 1–21.

—— 1931*f*. Whitney, 17. The birds of Malaita Island (British Solomon Islands). *Amer. Mus. Novit.* (504) : 1–26.

—— 1932*a*. Whitney, 18. Notes on Meliphagidae from Polynesia and the Solomon Islands. *Amer. Mus. Novit.* (516) : 1–30.

—— 1932*b*. Whitney, 19. Notes on the Bronze Cuckoo, *Chalcites lucidus*, and its subspecies. *Amer. Mus. Novit.* (520) : 1–9.

—— 1932*c*. Whitney, 20. Notes on thickheads (*Pachycephala*) from the Solomon Islands. *Amer. Mus. Novit.* (522) : 1–22.

—— 1932*d*. Whitney, 21. Notes on thickheads (*Pachycephala*) from Polynesia. *Amer. Mus. Novit.* (531) : 1–23.

—— 1933*a*. Whitney, 22. Three new genera from Polynesia and Melanesia. *Amer. Mus. Novit.* (590) : 1–6.

—— 1933*b*. On a collection of birds, supposedly from the Solomon Islands. *Ibis* (13) **3** : 549–552.

—— 1934*a*. Whitney, 28. Notes on some birds from New Britain, Bismarck Archipelago. *Amer. Mus. Novit.* (709) : 1–15.

—— 1934*b*. Whitney, 29. Notes on the genus *Petroica*. *Amer. Mus. Novit.* (714) : 1–19.

—— 1935. Whitney, 30. Descriptions of twenty-five new species and subspecies. *Amer. Mus. Novit.* (820) : 1–6.

—— 1936. Whitney, 31. Descriptions of twenty-five species and subspecies. *Amer. Mus. Novit.* (828) : 1–19.

MAYR, E. 1937. Whitney, 33. Notes on New Guinea birds. 1. *Amer. Mus. Novit.* (915) : 1–19.

—— 1938*a*. Whitney, 39. Notes on New Guinea birds. 4. *Amer. Mus. Novit.* (1006) : 1–16.

—— 1938*b*. Whitney, 40. Notes on New Guinea birds. 5. *Amer. Mus. Novit.* (1007) : 1–16.

—— 1940*a*. Whitney, 41. Notes on New Guinea birds. 6. *Amer. Mus. Novit.* (1056) : 1–12.

—— 1940*b*. Whitney, 43. Notes on New Guinea birds. 7. *Amer. Mus. Novit.* (1091) : 1–3.

—— 1941*a*. *List of New Guinea birds. A systematic and faunal list of the birds of New Guinea and adjacent islands.* New York ; A.M.N.H. : xi + 260 pp.

—— 1941*b*. [*recte* 1940]. Borders and subdivision of the Polynesian region as based on our knowledge of the distribution of birds. *Proc. Pacific Sci. Congr.* (6) **4** : 191–195. Berkley & Los Angeles ; U. Calif. P.

—— 1941*c*. Whitney, 45. Notes on New Guinea birds. 8. *Amer. Mus. Novit.* (1133) : 1–8.

—— 1941*d*. Whitney, 47. Notes on the genera *Halcyon*, *Turdus* and *Eurostopodus*. *Amer. Mus. Novit.* (1152) : 1–7.

—— 1942. *Systematics and the origin of species from the viewpoint of a zoologist. Columbia biological series* (13). New York ; Columbia U.P. : xiv + 334 pp.

—— 1944*a*. The birds of Timor and Sumba. *Bull. Amer. Mus. nat. Hist.* **83** (2) : 129–194.

—— 1944*b*. Timor and the colonization of Australia by birds. *Emu*, **44** : 113–130.

—— 1944*c*. Whitney, 54. Notes on some genera from the southwest Pacific. *Amer. Mus. Novit.* (1269) : 1–8.

—— 1944*d*. Wallace's Line in the light of recent zoogeographic studies. *Quart. Rev. Biol.* **19** : 1–14.

—— 1945*a*. *Birds of the southwest Pacific. A field guide to the birds of the area between Samoa, New Caledonia, and Micronesia.* New York ; Macmillan : xix + 316 pp.

—— 1945*b*. Whitney, 55. Notes on the birds of Northern Melanesia. 1. *Amer. Mus. Novit.* (1294) : 1–12.

—— 1948. Geographical variation in the Reed-Warbler. *Emu*, **47** : 205–210.

—— 1949*a*. Artbildung und Variation in der *Halcyon-chloris-Gruppe*. *Ornithologie als biologische Wissenschaft* : 55–60. Heidelberg : Universitätsverlag ; eds. Mayr & Schüz.

—— 1949*b*. Whitney, 57. Notes on the birds of Northern Melanesia. 2. *Amer. Mus. Novit.* (1417) : 1–38.

—— 1955. Whitney, 63. Notes on the birds of Northern Melanesia. 3. *Amer. Mus. Novit.* (1707) : 1–46.

—— 1957. Whitney, 64. Notes on the birds of Northern Melanesia. 4. *Amer. Mus. Novit.* (1823) : 1–14.

—— & AMADON, D. 1941. Whitney, 46. Geographical variation in *Demigretta sacra* (Gmelin). *Amer. Mus. Novit.* (1144) : 1–11.

—— —— 1947. A review of the Dicaeidae. *Amer. Mus. Novit.* (1360) : 1–32.

—— & CAMRAS, S. 1938. Birds of the Crane Pacific Expedition. *Publ. Field Mus.* (*Zool.*) **20** (34) : 453–473.

—— & MOYNIHAN, M. 1946. Evolution in the *Rhipidura rufifrons* group. *Amer. Mus. Novit.* (1321) : 1–21.

—— & RAND, A. L. 1937. Results of the Archbold Expeditions. 14. The birds of the 1933–1934 Papuan Expedition. *Bull. Amer. Mus. nat. Hist.* **73** (1) : 1–248.

—— & RIPLEY, S. D. 1941. Whitney, 44. Notes on the genus *Lalage* Boie. *Amer. Mus. Novit.* (1116) : 1–18.

—— & SCHAUENSEE, R. M. DE. 1939. Zoological results of the Denison-Crockett Expedition to the South Pacific for the Academy of Natural Sciences of Philadelphia, 1937–1938. 1. The birds of the island of Biak. *Proc. Acad. nat. Sci. Philad.* **91** : 1–37.

—— & VAURIE, C. 1948. Evolution in the family Dicruridae (birds). *Evolution*, **2** : 238–265.

MEES, G. F. 1955. The name of the white-eye from Rendova Island (Solomon Islands). *Zool. Meded.* **33** (28) : 299–300.

—— 1961. A systematic review of the Indo-Australian Zosteropidae. 2. *Zool. Verh., Leiden* (50) : 1–168.

MEYER, O. 1927. Zur Ornithologie des Bismarckarchipels. *Orn. Mber.* **35** : 112–113.
—— 1930. Uebersicht über die Brutzeiten der Vögel auf der Insel Vuatom (New Britain). *J. Orn.* **78** : 19–38.
—— 1933. Vögeleier und Nesten aus Neubritannien, Südsee. *Beitr. FortPflBiol. Vögel,* **9** : 122–136, 182–185.
—— 1937. Australische Zugvögel im Bismarckarchipel. *Orn. Mber.* **45** : 48–51.
OGILVIE-GRANT, W. R. 1887. A list of the birds collected by Mr. Charles Morris Woodford in the Solomon Archipelago. *Proc. zool. Soc. Lond.* 1887 : 328–333.
—— 1888. Second list of the birds collected by Mr. C. M. Woodford in the Solomon Archipelago. *Proc. zool. Soc. Lond.* 1888 : 185–204.
—— 1914. [Description of two new subspecies of kingfishers from the Solomon Islands.] *Bull. Brit. Orn. Cl.* **35** : 13–14.
PENDLETON, R. C. 1947. Field observations on the Spotted Button-Quail on Guadalcanal. *Auk,* **64** : 417–421.
PETERS, J. L. 1935. Remarks on the avian genus *Eos. Proc. biol. Soc. Wash.* **48** : 67–70.
RAMSAY, E. P. 1879*a*. Notes on zoology of the Solomon Islands. 1. Aves. *Proc. Linn. Soc. N.S.W.* (1) **4** : 65–84.
—— 1879*b*. Notes on some recently described birds from the Solomon Islands. *Proc. Linn. Soc. N.S.W.* (1) **4** : 313–315.
—— 1880. Contributions to the zoology of New Guinea. 6. On some new and rare birds, from south east coast of New Guinea, &c. *Proc. Linn. Soc. N.S.W.* (1) **4** : 464–470.
—— 1881. Notes on the zoology of the Solomon Islands, with descriptions of some new birds. 2. *Proc. Linn. Soc. N.S.W.* (1) **6** : 176–181.
—— 1882*a*. Notes on the zoology of the Solomon Islands, with descriptions of some new birds. *Proc. Linn. Soc. N.S.W.* (1) **6** : 718–727.
—— 1882*b*. Descriptions of two new birds from the Solomon Islands. *Proc. Linn. Soc. N.S.W.* (1) **6** : 833–835.
—— 1882*c*. Notes on the zoology of the Solomon Islands. 4. *Proc. Linn. Soc. N.S.W.* (1) **7** : 16–43.
—— 1882*d*. Descriptions of two new birds from the Solomon Islands. *Proc. Linn. Soc. N.S.W.* (1) **7** : 299–301.
—— 1882*e*. Descriptions of some new birds from the Solomon Islands and New Britain. *J. Linn. Soc. (Zool.),* **16** : 128–131.
—— 1883. Notes on birds from the Solomon Islands. *Proc. Linn. Soc. N.S.W.* (1) **7** : 665–673.
RAND, A. L. 1938. Results of the Archbold Expeditions. 19. On some non-passerine New Guinea birds. *Amer. Mus. Novit.* (990) : 1–15.
RIPLEY, S. D. 1941. Notes on the genus *Coracina. Auk,* **58** : 381–395.
—— 1942. The species *Eurystomus orientalis. Proc. biol. Soc. Wash.* **55** : 169–176.
—— 1959. Competition between sunbird and honeyeater species in the Moluccan islands. *Amer. Nat.* **93** : 127–132.
—— 1961. Aggressive neglect as a factor in interspecific competition in birds. *Auk,* **78** : 366–371.
—— & BIRCKHEAD, H. 1942. Whitney, 51. On the fruit pigeons of the *Ptilinopus purpuratus* group. *Amer. Mus. Novit.* (1192) : 1–14.
ROTHSCHILD, W. 1904. [On a new species of *Centropus* from the Solomon Islands.] *Bull. Brit. Orn. Cl.* **14** : 59.
—— & HARTERT, E. 1901*a*. Notes on Papuan birds. *Novit. Zool.* **8** : 55–88, 102–162.
—— —— 1901*b*. List of a collection of birds from Kulambangra and Florida Islands, in the Solomons group. *Novit. Zool.* **8** : 179–189.
—— —— 1901*c*. List of a collection of birds from Guadalcanar Island, in the Solomon group. *Novit. Zool.* **8** : 373–382.
—— —— 1902. List of a collection of birds made on Ysabel Island in the Solomon group by Mr. A. S. Meek. *Novit. Zool.* **9** : 581–594.
—— —— 1905. Further contributions to our knowledge of the ornis of the Solomon Islands. *Novit Zool.* **12** : 243–268.

ROTHSCHILD, W. 1907. Notes on Papuan birds. *Novit. Zool.* **14** : 433–446.

—— —— 1908*a*. The birds of Vella Lavella, Solomon Islands. *Novit. Zool.* **15** : 351–358.

—— —— 1908*b*. On a collection of birds from San Cristoval, Solomon Islands. *Novit. Zool.* **15** : 359–365.

—— —— 1914. The birds of the Admiralty Islands, north of German New Guinea. *Novit. Zool.* **21** : 281–298.

—— —— 1916. On some forms of *Coracina* (*Graucalus* auct.) from the Solomon Islands. *Novit. Zool.* **23** : 289–291.

SALOMONSEN, F. 1960. Notes on flowerpeckers (Aves, Dicaeidae). 3. The species group *Dicaeum concolor* and the superspecies *Dicaeum erythrothorax*. *Amer. Mus. Novit.* (2016) : 1–36.

SANFT, K. 1960. Aves/Upupae. Bucerotidae. *Tierreich* (76) : [4] + 1–174.

SCHONWETTER, M. 1935. Vogeleier aus Neubritannien. *Beitr. FortPflBiol. Vögel*, **11** : 129–136.

SCLATER, P. L. 1869. On a collection of birds from the Solomon Islands. *Proc. zool. Soc. Lond.* 1869 : 118–126.

SCOTT, W. E. 1946. Birds observed on Espiritu Santo, New Hebrides. *Auk*, **63** : 362–368.

SHARPE, R. B. 1883. Notes on some species of birds of the family Dicaeidae. *Proc. zool. Soc. Lond.* 1883 : 578–580.

—— 1888. Descriptions of some new species of birds from the island of Guadalcanar in the Solomon Archipelago, discovered by Mr. C. M. Woodford. *Proc. zool. Soc. Lond.* 1888 : 182–185.

SIBLEY, C. G. 1946. [Four notes on Northern Melanesian birds.] *Condor*, **48** : 92–93, 97, 182, 281–282.

—— 1951. Notes on the birds of New Georgia, central Solomon Islands. *Condor*, **53** : 81–92.

SIMS, R. W. 1954. A new race of button-quail (*Turnix maculosa*) from New Guinea. *Bull. Brit. Orn. Cl.* **74** : 37–40.

STICKNEY, E. H. 1943. Whitney, 53. Northern shore birds in the Pacific. *Amer. Mus. Novit.* (1248) : 1–9.

STRESEMANN, E. 1912. Ornithologische Miszellen aus dem indo-australischen Gebiet. *Novit. Zool.* **19** : 311–351.

—— 1913. Ornithologische Miszellen aus dem indo-australischen Gebiet. 2. *Novit. Zool.* **20** : 289–324.

—— 1914. Die Vögel von Seran (Ceram). (Aus den zoologischen Ergebnissen der II Freiburger Molukken-Expedition). *Novit. Zool.* **21** : 25–153.

—— 1921. [Neuen Formen aus dem Stromgebiet des Sepik (nördliches Neuguinea) und aus Neupommern.] *Anz. orn. Ges. Bayern*, **1** : 33–38.

—— 1923. Dr. Bürgers' ornithologische Ausbeute im Stromgebeit des Sepik. Ein Beitrag zur Kenntnis der Vogelwelt Neuguineas [concluded]. *Arch. Naturgesch.* **89**A (8) : 1–92.

—— 1933. Neue Vogelrassen von Lihir (Bismarck-Archipel). *Orn. Mber.* **41** : 114–116.

—— 1939. " Heterogynie " im Rassenkreis *Edolisoma morio*. *Orn. Mber.* **47** : 124–126.

SUTTER, E. 1955. Über die Mauser einiger Laufhühnchen und die Rassen von *Turnix maculosa* und *sylvatica* im indo-australischen Gebiet. *Verh. naturf. Ges. Basel*, **66** : 85–139.

TIMES ATLAS, 1958. *The Times atlas of the world. Mid-century edition.* **1.** London ; Times Publishing Co. : xxvii + 24 pp, 24 pls.

TRISTRAM, H. B. 1879. On a collection of birds fom the Solomon Islands and New Hebrides. *Ibis* (4) **3** : 437–444.

—— 1882. Notes on a collection of birds from the Solomon Islands, with descriptions of new species. *Ibis* (4) **6** : 133–146.

—— 1892. On two small collections of birds from Bugotu and Florida, two of the smaller Solomon Islands. *Ibis* (6) **4** : 293–297.

—— 1894. On some birds from Bugotu, Solomon Islands, and Santa Cruz. *Ibis* (6) **6** : 28–31.

—— 1895. Further notes on birds from Bugotu, Solomon Islands, with description of a new species. *Ibis* (7) **1** : 373–376.

TUBB, J. A. 1945. Field notes on some New Guinea birds. *Emu*, **44** : 249–273.

VANE, E. N. T. 1959. Some observations on the Cacatuinae—the cockatoos. *Avicult. Mag.* 1959 : 9–16.

VAURIE, C. 1949. A revision of the bird family Dicruridae. *Bull. Amer. Mus. nat. Hist.* **93** (4) : 199–342.

—— 1958. Remarks on some Corvidae of Indo-Malaya and the Australian region. *Amer. Mus. Novit.* (1915) : 1–13.

VERHEYEN, R. 1956. Analyse du potentiel morphologique et projet d'une nouvelle classification des Psittaciformes. *Bull. Inst. Sci. nat. Belg.* **32** (55) : 1–54.

VIRTUE, R. M. 1947. Birds observed at Torokina, Bougainville Island. *Emu,* **46** : 324–331.

VÖLKER, O. 1953. Das Farbkleid der Flaumfusstauben (Ptilinopodinae). *J. Orn.* **94** : 263–273.

VOOUS, K. H. & MARLE, J. G. VAN. 1949. The distributional history of *Coracina* in the Indo-Australian archipelago. *Bijdr. Dierk.* **28** : 513–529.

WALKER, F. S. 1948. *The forests of the British Solomon Islands Protectorate.* London ; Crown Agents : 186 pp. (+corr. and add. 1950).

WHITE, C. N. M. 1936. [Note on the Australian Tree-Martin *Petrochelidon nigricans.*] *Bull. Brit. Orn. Cl.* **56** : 90–92.

—— 1938. [Notes on some Solomon Island birds.] *Bull. Brit. Orn. Cl.* **58** : 46–48.

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BY

P. J. P. WHITEHEAD

Department of Zoology, British Museum (Nat. Hist.)

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ABSTRACT

The three genera of Indo-Pacific Dorosomatidae with filamentous last dorsal rays have been examined. Although closely related, *Clupanodon* and *Konosirus* are here separated from *Nematalosa* and from each other on a number of characters, including the shape of the suboperculum and jaw form. There seems to be little justification for placing the Australian species in the genus *Fluvialosa*, and all are here referred to *Nematalosa*. *N. arabica* is redescribed from specimens now in the Museum collection.

1. INTRODUCTION

WHILE identifying specimens of *Nematalosa arabica* Regan from the Somalia coast and the Gulf of Aden, I noticed that no further description of this species has been made since Regan's (1917) description of the holotype. But in redescribing *N. arabica*, it was necessary to make comparisons not only with other species of *Nematalosa*, but also with the monotypic genera *Clupanodon* and *Konosirus*, the last in some respects an annectant form between the other two. The result of this comparison has been to reinforce the view of Herre & Myers (1931) that *K. punctatus* (Schlegel) is generically distinct from *Clupanodon thrissa* (Linn.), but that it should not be relegated to *Nematalosa*. The latter genus shows some variation, especially in lower jaw shape, but there are too many intergrading forms for any but specific divisions to be considered.

2. *NEMATALOSA* AND ITS ALLIES IN THE INDO-PACIFIC

Seven species are included under this heading (eight if *Nematalosa elongata* (Macleay) is accepted). All have an elongated last dorsal ray and a single supplemental or supra-maxilla. Although the importance of an elongated dorsal ray is perhaps over-rated, I have here omitted consideration of the two Indo-Pacific dorosomatid genera lacking a filamentous ray, *Gonialosa* and *Anodontostoma*. Regan (1917) proposed *Nematalosa* for those species (until then included in *Chatoessus* Cuvier), which in addition to possessing a dorsal filament and single supra-maxilla, also had a flared or reflected edge to the dentary ; two related forms without flared dentaries he placed in *Clupanodon* Lacépède (*C. thrissa* (Osbeck) and *C. punctatus* (Schlegel)), putting *Konosirus* Jordan & Snyder in the synonymy of *Clupanodon.*

However, Herre & Myers (1931) stated that the dentary in *C. punctatus* is to some extent reflected as in *Nematalosa*, but that *C. punctatus* differs sufficiently in other respects from *Nematalosa*, as well as from *Clupanodon*, to justify a monotypic genus, *Nealosa* (suppressed (Myers, 1932) since *Konosirus* had already been applied to *punctatus*). *Konosirus* has frequently been placed in the synonymy of *Clupanodon* (e.g. Fowler, 1941, Roxas, 1934) or again considered of subgeneric standing only, but some authors have recognized it (Iwai, 1956).

After examining material in this museum, I conclude that the criteria used by Herre & Myers to separate *Konosirus* are valid and should be re-emphasized. To them can be added also the rather higher vertebral count in *K. punctatus*, e.g. :

K. punctatus . .	48, 50, 51
C. thrissa . .	43
N. arabica . .	46
N. erebi . .	43*

(Also *Anodontostoma* 42 ;* *Gonialosa* 44,* 46.*

Clupanodon thrissa is unique in this group in having the outer demibranchs of the first two arches very short, about half the length of the corresponding inner demibranchs, and this character, together with its normal [non-flared] dentary and its subopercular shape (see below), clearly distinguish it from *Nematalosa*. But if such differences merit generic distinction, then the high vertebral count in *Konosirus punctatus* as well as its flared dentary and normal demibranchs must be sufficient reason to separate it generically from *Clupanodon*, while its subopercular shape and proportions of maxilla and premaxilla must distinguish it from *Nematalosa*. The characters on which this argument is based are discussed separately below.

Of the species normally placed in *Nematalosa*, four require little comment. *N. arabica* Regan and *N. japonica* Regan occupy the western and eastern limits of the range of this genus (i.e. Red Sea to Japan), *N. nasus* (Bloch) occurs in the central part of this region (India and Burma) and *N. come* (Richardson) is a Western Australian species. The remaining species, all Australian, have been placed in *Fluvialosa*, a genus proposed by Whitley (1943) for *Chatoessus elongatus* Macleay, *N. horni* (Zeitz) and *N. richardsoni* (Castelnau), and later (Whitley, 1948) for *F. paracome* Whitley and *F. bulleri* Whitley, and again (Whitley, 1956) for *N. erebi* (Günther). These species can all be adequately accommodated in Regan's *Nematalosa*, but they were distinguished by Whitley as being " large fluviatile or estuarine Australian herrings " as opposed to the genotype of *Nematalosa* " the marine *Clupea nasus* Bloch " (Whitley, 1943).

---

* Figures from Regan (1917).

As will become apparent in later discussion, *N. horni* and *N. erebi* are rather distinctive in comparison with other species of *Nematalosa*, especially in their greater body depth, few ventral scutes and jaw shape. On the other hand the species which most nearly approaches these Australian forms is none other than the " marine " *N. nasus*. Certainly the Australian forms cannot be separated from the rest with the same confidence as in the case of *Konosirus* or *Clupanodon*. I consider it reasonable, therefore, to place *Fluvialosa* in the synonymy of *Nematalosa*.

Whereas *N. horni* and *N. erebi* appear to be valid species, *N. richardsoni* is problematical. It was originally described as a smaller fish than *N. erebi*, with an average length of 7 inches (Castelnau, 1873), but Macleay (1880) refers to it as attaining 10–14 inches. Unfortunately the descriptions of both these authors are too vague to distinguish this species from *N. erebi*, and its distinctive features (dorsal filament short, body more slender) may be juvenile characters or characters whose growth shows positive allometry with standard length. Fowler (1941) places *N. richardsoni* in synonymy with *N. come*, together with *N. erebi* and *N. horni*, but this seems unjustifiable " lumping " since the latter two at least, differ from *N. come* in numbers of scutes and dorsal rays and mouth shape. I have not seen specimens of *N. elongata*, but descriptions suggest a species very close to, if not identical with *N. horni*.

The two remaining species, *N. paracome* and *N. bulleri* are also unrepresented in the museum collections. The former, described from a single specimen, is said to differ from other species in having no humeral blotch (although a " faint duskiness " is described) ; a shorter dorsal filament (although as a percentage of standard length it differs by only 1·7 per cent. from that of *N. bulleri* according to actual measurements given by Whitley, 1948) ; and fewer predorsal and lateral scales (respectively two and four fewer than in *N. bulleri*).

The Australian species have not been described sufficiently critically for comparisons to be made on the basis of descriptions alone. All however, have rather fewer scale and scute counts than do the other Indo-Pacific species, and (except for *N. elongata*) all are rather deep-bodied fishes. It seems probable that all have the flared dentary and rather inferior mouth characteristic of *N. erebi* and *N. horni*. But although these Australian fishes form a fairly distinctive group, they are none the less linked by *N. come* and *N. nasus* to the remaining Indo-Pacific species ; there is no definite point at which the genus *Fluvialosa* could be said to have begun, and until more studies have been made of the Australian species, all should be placed in *Nematalosa*.

3. DIAGNOSTIC FEATURES

Before assessing further the relationships of *Nematalosa*, *Konosirus* and *Clupanodon*, eight principal characters must be discussed on which specific and generic divisions have been made.

(i) *Gill Filaments*

In *C. thrissa* alone the outer demibranchs of the first two arches are only half the length of the inner demibranchs; in the remaining species the outer demibranchs are at least three-quarters (usually more) of the inner series. The difference is quite striking and appears to be constant, and it seems to be a strong factor against including *K. punctatus* in *Clupanodon*.

(ii) *Gillrakers*

In *C. thrissa* and *K. punctatus* the longest gillrakers on the lower part of the anterior arch are at least three-quarters the length of the gill filaments opposite. In all other species the gillrakers are approximately half the length of the gill filaments, often less.

(iii) *Parietal Sculpture*

In all species in this group there is a flat, longitudinally striated, wedge-shaped area at the back of the skull formed partly of the parietals, but to which a postero-lateral edge of the frontals also contributes. This area is only lightly covered with skin. The striations conform to two general types, referred to here as the *sardinella* pattern and the *harengula* pattern (in which two genera they are best developed amongst the clupeids). In the former there are 5–10 striae running almost the entire length of the exposed bony area, and posteriorly there is usually a well-defined transverse bony ridge. This type occurs in *N. come* (see Text-fig. 1*a*), *N. japonica*, *N. nasus*, and usually but not invariably in *N. horni*. The *harengula* pattern normally lacks the transverse ridge, or it is less prominent, and the longitudinal striae are much fewer (about 3–5) and often discontinuous. This occurs in *C. thrissa, K. punctatus* and *N. arabica* (see Text-fig. 1*b*).

It is difficult to assess the importance of these patterns, and especially since even in *Harengula* and *Sardinella* there are a few exceptions (thus *H. nymphaea* has 8–10 striae). Certainly *N. arabica* more closely approaches *C. thrissa* and *K. punctatus* in jaw structure than do any of the species with a *harengula* pattern. *N. japonica* on the other hand shows a striation pattern in some respects intermediate between the *harengula* and the *sardinella* types. There is also some variation with age.

(iv) *Scutes*

The total number of ventral scutes does not vary much between the three genera (range 28–36) and there is considerable overlap between species. Nonetheless certain trends are apparent when pre- and post-pelvic scutes are considered separately.

In the pre-pelvic series the Australian species (Whitley's *Fluvialosa*) have a consistently lower count. In the post-pelvic series, as well as in the total count, *K. punctatus*, *N. japonica* and *N. arabica* all have a rather high count in comparison with the Australian species. Rather surprisingly *C. thrissa* falls within the latter group. Apart from this exception, scute numbers tend to confirm the rather distinctive character of the Australian species, although there is no clear division and *C. thrissa* appears to be intermediate between the two groups.

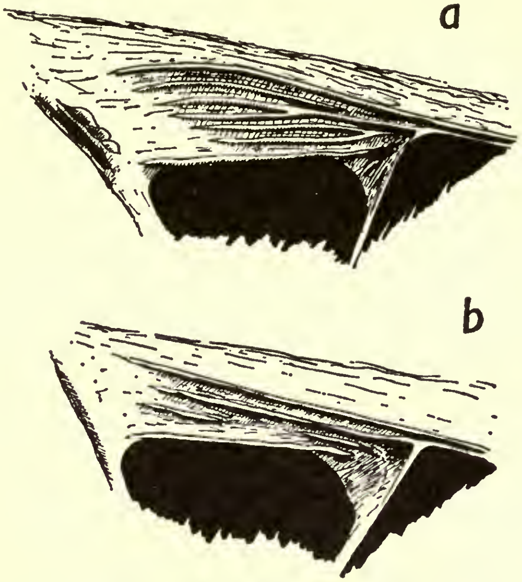

Fig. 1. Two types of parietal sculpture, right lateral view.
(a) *Nematalosa come* (the '*sardinella*' type).
(b) *Nematalosa arabica* (the '*harengula*' type).
For explanation see text.

Table I.—*Ventral Scutes in Certain Indo-Pacific Dorosomatidae*

	Pre-pelvic	Post-pelvic	Total	Number of Specimens
Clupanodon thrissa	(17) 18 (19)*	11–12	(28) 29–30 (31)	5
Konosirus punctatus	(17) 18–19 (20)	15–16	(32–33) 34–35 (36)	13†
Nematalosa arabica	(18)19	(13) 14 (15)	(32) 33 (34)	9†
N. japonica	18	14–16	32–34	3†
N. nasus	18	11–13	29–31	5
N. come	18	12–13	30–31	5†
N. erebi	16–17	11–14	28–31	5
N. horni	16–17	12–13	28–30	5†
N. elongata ‡	17	11	28	1

* Parentheses indicate single instance.
† Including the type(s).
‡ Based on Whitley (1943).

(v) *Suboperculum*

Herre & Myers (1931) first noticed that the shape of the exposed portion of the suboperculum in *C. thrissa* and *K. punctatus* differed from that of related species. In these two species it is far less rectangular (see Text-figs. 3*a* and *b*). In fact, this difference in shape is not only a difference in posterior outline of the suboperculum, but results also from the angle made by the lower edge of the operculum with the

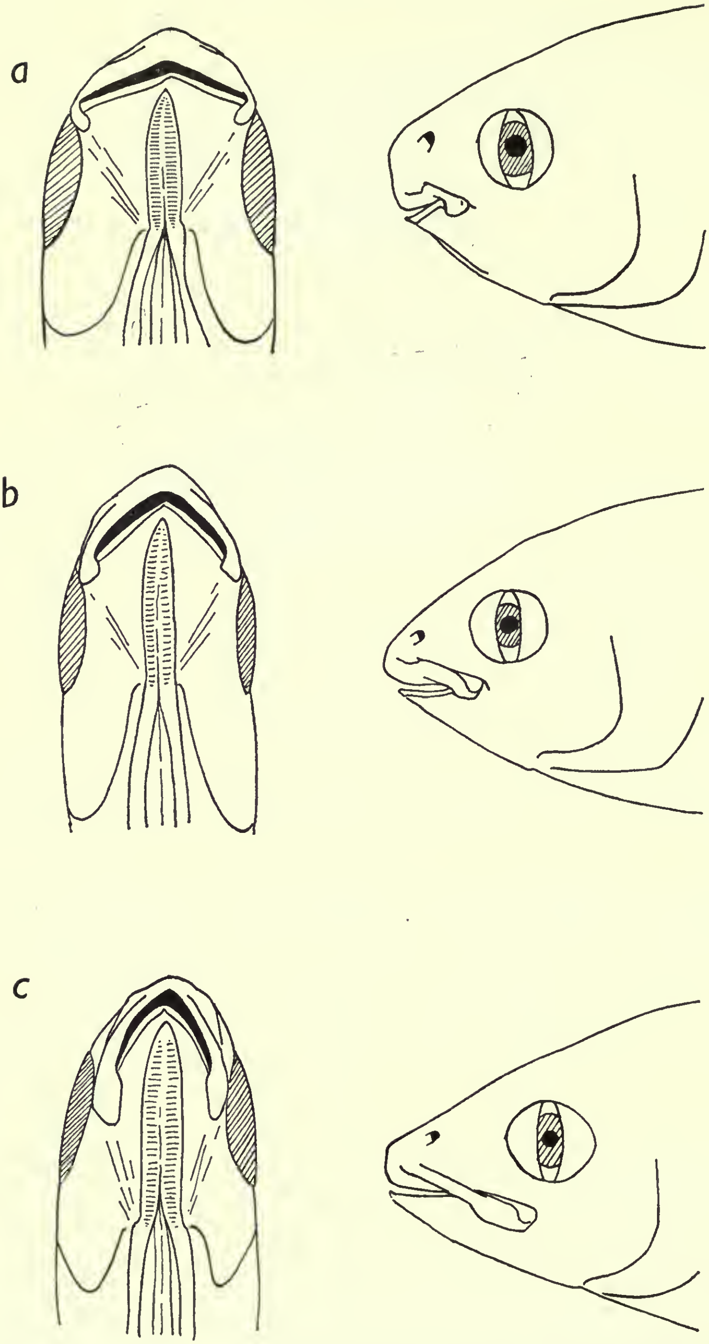

FIG. 2. A comparison between the short and rather wide jaws of (a) *Nematalosa horni* (specimen 140 mm.), the longer and narrower jaws of (c) *Clupanodon thrissa* (172 mm.), and the intermediate condition found in (b) *Nematalosa arabica* (150 mm.). Ventral and lateral views.

posterior margin of the inter-operculum. In *C. thrissa* and *K. punctatus* this angle is obtuse, but in the others it approaches a right-angle. The difference appears to be consistent in fishes of all sizes.

(vi) *Dorsal rays*

In dorsal (and anal) fin ray counts there is some advantage in counting branched and unbranched rays separately. Thus some species may be distinguished by a small but constant difference of only one or two rays, but where the first and second unbranched rays are small or even minute, this difference may be missed.

Regan (1917) separated *N. horni* and *N. erebi* from other species because of their low dorsal count. In the following table this low count is shown to result mainly from a low branched ray count.

TABLE II.—*Branched and Unbranched Dorsal Rays in Certain Species of Dorosomatidae*

	Unbranched	Branched	Total	Number of Specimens
N. arabica	4–5	(12)* 13–14	17–18	8†
N. japonica	4	13 (14)	17 (18)	3†
N. nasus	4–5	12–13	(16) 17 (18)	4
N. come	4	13 (14)	17 (18)	8†
N. erebi	(3) 4	10–11	14–15	12†
N. horni	3–4	9–11 (12)	13–15	10†

* Single instances in parentheses.
† Including the type(s).

Apart from *N. horni* and *N. erebi*, the remaining species are remarkably alike in this character.

(vii) *Upper and Lower Jaws*

Between *Clupanodon thrissa* and *Nematalosa horni* there exists a graduated series of jaw forms in which the species can be arranged in the following order.

Clupanodon thrissa
Konosirus punctatus
Nematalosa arabica
N. come and *N. japonica*
N. nasus
N. horni, *N. erebi* (and if valid, *N. elongata*)

This series consists of a progressive shortening of the upper jaw elements, a deepening of the premaxilla, a more inferior mouth, a widening of the dentary and flaring of its outer edge (especially at the corners of the mouth), and an increasingly wide angle made by the dentaries at their symphysis. Three stages in this series are shown in Text-fig. 2*a*, *b* and *c*.

As Herre & Myers (1931) noted, the expanded portion of the maxilla (i.e. the distal end) is in *Clupanodon* and *Konosirus* rather elongated and extends as far beyond the premaxilla tip as the length of the premaxilla itself; with the inclusion of the supramaxilla, the expanded portion of the maxilla becomes approximately rectangular, the length of the expanded portion comprising a half to two thirds of the whole length of the maxilla. From the specimens available it appears that the maxilla in *K. punctatus* does not quite attain the length found in *C. thrissa*, but is almost exactly intermediate in this respect between the latter and *N. arabica* (in which the expanded portion is contained 2½–3½ times in the length of the maxilla). *N. come* and *N. japonica* represent a further reduction in the length of the expanded portion as well as a trend towards a downwardly directed tip to the maxilla. In *N. nasus*, and to a greater extent in the Australian species, this latter trend is further accentuated by a turning inwards of the maxilla tip round the flared corners of the lower jaw. The series shows a reduction of the narrow stem of the supra-maxilla and the premaxilla becomes shorter and slightly deeper.

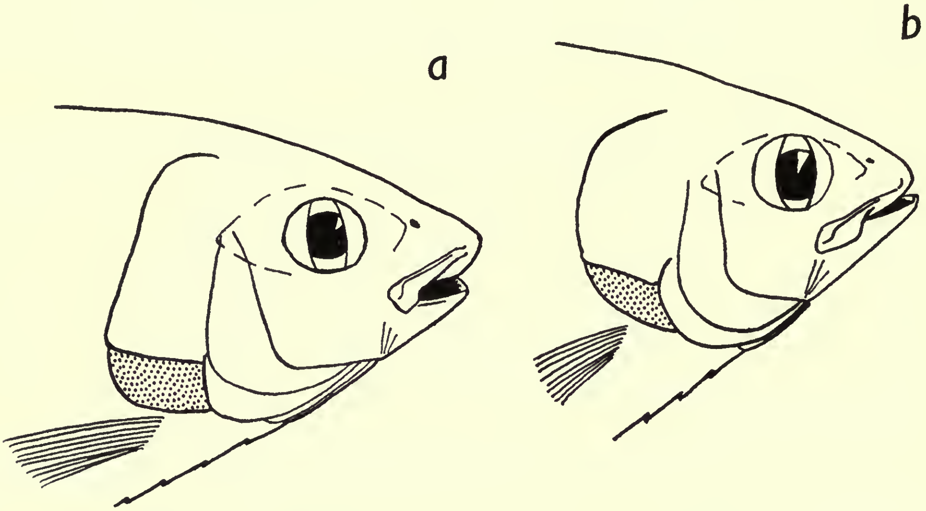

FIG. 3. The shape of the exposed portion of the suboperculum (stippled), determined in part by the angle formed by the lower edge of the operculum and the posterior edge of the interoperculum.
(a) *Nematalosa arabica* (150 mm. specimen).
(b) *Clupanodon thrissa* (180 mm. specimen).

The series also shows a shortening of the lower jaw (from dentary symphysis to quadrate articulating facet), and at the same time the mouth, when viewed ventrally, becomes wider and more nearly a straight transverse line (see Text-fig. 2). With the flaring of the dentary, the lower jaw is no longer included in the upper when the mouth is closed.

With these changes comes a slight shortening of the snout, the head in profile becoming deeper and less acutely pointed anteriorly.

Although specimens of *N. horni* or *N. erebi* seem to differ strikingly in mouth shape from say *C. thrissa*, the difference is one of degree only and the remaining species provide almost perfect intermediate steps. Once again there is no basis for separating the Australian species.

(viii) *Second Sub-orbital*

Normally the second sub-orbital extends to about the centre of the orbit and its anterior border forms a diagonal (Text-fig. 4*a*). In *N. nasus*, however, this bone covers the entire cheek, terminating in front of the eye, and its anterior border is vertical (Text-fig. 4b). This single exception is not related to any of the other trends found.

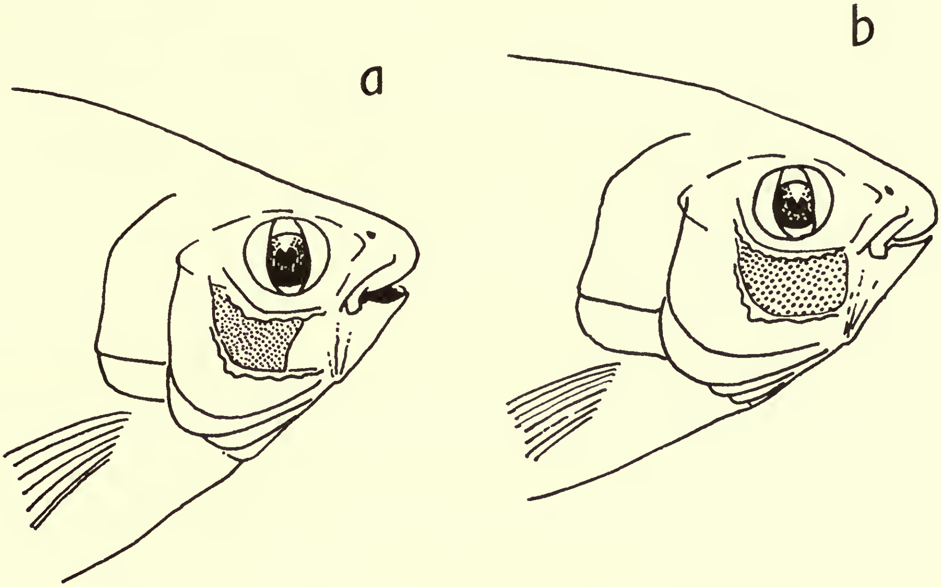

FIG. 4. The shape and extent of the second suborbital (stippled).

(a) *Nematalosa come* (129 mm.).

(b) *Nematalosa nasus* (115 mm.).

4. DISCUSSION

Of the characters discussed, jaw form shows the most complete transition, with a perfectly graded series between the "normal" jaw of *Clupanodon thrissa* and the pronounced inferior jaws of *Nematalosa erebi* and *N. horni*. This series may reflect a progressive trend towards bottom-feeding, for the mouth shape of the Australian species strongly resembles that of the iliophagous grey mullets ; unfortunately there are insufficient records of food and feeding habits to confirm this.

To what extent do other characters conform to this series ? Comparing the tables given for dorsal rays, vertebrae and pre- and post-pelvic scutes, exactly the same order of species can be maintained with one exception ; *C. thrissa* has unexpectedly low vertebral and post-pelvic scute counts if it is to head the series. However, this does not seem to be a strong objection to the order of the species and may well represent a variation similar to the unique sub-orbital shape in *N. nasus*.

As a whole, species in this group show a great number of similarities and common features, and there is something to be said for placing all in a single genus, perhaps giving *C. thrissa* subgeneric status. But there are several rather distinctive features found in one, two, or at the most three species only, which appear to be unrelated to the general trend found in mouth shape or meristic characters. Thus the differences in gillraker and gill filament length, and the shape of the suborbital and subopercular bones serve to fragment the group.

Two main evolutionary trends are apparent. The first, which can be broadly linked with geographical distribution, involves mouth shape and certain meristic characters, and shows a gradual transition from one species to the next. The second, apparently unrelated to distribution, shows no intermediates and appears to represent merely variations in individual species or species pairs. Thus within the group, there is a reasonably complete series between *N. horni* and *N. arabica*, but there is a distinct break between these and *C. thrissa* and *K. punctatus*, which themselves can be clearly separated.

In the first group of characters (those which intergrade) it is difficult to decide whether the non-meristic series (i.e. jaw form) should be accorded the same status as the meristic series. Thus, there is good reason to suspect that scute, finray and vertebral numbers can be correlated with distribution (i.e. with an extrinsic factor such as temperature), whereas with jaw shape, these may be merely representative stages in the evolution of the group. That the species can be arranged in the same order in respect to both these kinds of character may be coincidental.

In the second, or non-intergrading, group of characters, the differences between the species are often rather greater than one would expect, and it is perhaps surprising to find the aberrant form so often represented by only one or two species. Taken in conjunction with the intergrading series, the impression gained is of a group in which a few well adapted forms have survived, showing little tendency to speciate except amongst the Australian fishes, which are the most specialized and perhaps the most recent. *K. punctatus* (with a slightly higher vertebral count) and *C. thrissa* are probably the primitive members of the group.

5. A REDESCRIPTION OF *NEMATALOSA ARABICA* REGAN 1917

This description is based on the holotype (131 mm. S.L., B.M. (N.H.) No. 1887.11.11.312); a specimen from Mukalla labelled *N. nasus* (150 mm. S.L., B.M. (N.H.) No. 1945.12.31.14); and six specimens from Jibuti, Somaliland (94–101 mm. S.L., B.M. (N.H.) No. 1962.3.13.1–6).

Description

In percentages of standard length (S.L.): head length* 29·3–31·7, head depth at occiput 23·4–26·0, body depth 36·0–40·5, snout length 6·1–7·6, eye diameter 7·3–7·8, post-orbital† 13·9–15·3, premaxillary length 4·5–5·7, maxillary length 6·5–8·2, pectoral length 20·5–23·0, pelvic length 12·4–14·0, length of anal base

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* Premaxillary symphysis to posterior edge of suboperculum, i.e. not a horizontal line. This obviates measuring to inclined operculum edge.

† These last three measurements are taken in a straight line through the eye and therefore do not *in toto* equal head length.

15·3–17·9, pre-dorsal distance 49·0–51·0, pre-pelvic distance 52·0–54·5, length of last (filamentous) dorsal ray 35·5–41·0, depth of caudal peduncle (11·0) 12·1–12·9.

Premaxilla 1·14–1·77 times in length of maxilla; the length of the expanded portion of the maxilla 2·40–3·40 times in the length of the whole bone, the depth of the expanded portion 2·57–3·13 times in maxilla length. Maxilla tip reaching to below anterior pupil border.

Gill rakers about half length of gill filaments on anterior arch; outer demibranch equal or subequal to inner demibranchs.

42–45 scales in lateral series, 19 in transverse series. Ventral scutes 18–19 + 13–15 (total 32–34). Dorsal iv–v, 12–14 (total 17–18); anal ii–iii, 15–17 (total 18–20). Vertebrae 46 (1 specimen).

Pelvic fin base lies below 2nd or 3rd branched dorsal ray. Pectoral tips reach or almost reach pelvic fin base.

Angle between posterior margin of inter-operculum and ventral margin of operculum forming a right-angle, the sub-operculum appearing roughly rectangular (Text-fig. 3*a*). Parietal striae 3–5 (Text-fig. 1*b*). Mouth inferior, the dentary moderately expanded and reflected outwards (but not as strongly as in *N. come*) as shown in Text-fig. 2*b*.

6. GENERIC DIAGNOSES

In view of the foregoing comments on the three Indo-Pacific dorosomatid genera with filamentous last dorsal rays, more precise generic definitions can be given.

Nematalosa Regan

Nematalosa Regan, 1917, *Ann. Mag. nat. Hist.* (8) **19**: 313. (Type *Clupea nasus* Bloch, designated by Jordan, 1920, Genera of Fishes, Pt. 4, p. 560).
Fluvialosa Whitley, 1943, *Aust. Zool.* **10** (2): 170.

Indo-Pacific dorosomatid fishes with the last dorsal ray produced into a filament. Mouth subterminal or inferior; premaxilla short but deep; maxilla slender, expanded distally and curved both downwards and slightly inwards round the dentary; a single supramaxilla; dentaries meeting at their symphysis at an obtuse angle, forming sometimes an almost transverse cleft, the edge of each dentary flared or reflected outwards. Second suborbital with diagonal front border leaving an exposed area above the lower limb of the preoperculum (Text-fig. 4*a*) except in *N. nasus*, in which the front border is vertical (Text-fig. 4*b*). Suboperculum rectangular, the anterior and upper borders of the exposed portion forming an approximate right angle and the posterior margin angular and not smoothly rounded (Text-fig. 3*a*). Gillrakers on first arch half or less than half the length of the corresponding gill filaments; outer demibranchs on all arches at least threequarters of the length of the inner demibranchs.

Dorsal rays iii–iv, 9–14, anal rays 18–24 (of which the first two or three are unbranched), pelvic rays 8. Scales, 42–50 in lateral series, 14–21 transversely. Ventral scutes, 16–19 pre-pelvic, 11–16 post-pelvic, total 28–34.

Six species of *Nematalosa* are recognized here, *N. arabica*, *N. japonica*, *N. come*, *N. nasus*, *N. erebi* and *N. horni*.

Clupanodon Lacépède

Clupanodon Lacépède, 1803, *Hist. Nat. Poiss.*, **5** : 465. (Type *Clupea thrissa* Linnaeus, designated by Bleeker, 1866–72, *Atlas Ichth. Ind. Neerland*, **6** : 112).
Thrissa Rafinesque, 1815, *Analyse de la nature*, p. 88.

Indo-Pacific dorosomatid fishes with the last dorsal ray prolonged into a filament. Mouth subterminal ; premaxilla short but less deep than in *Nematalosa*, maxilla slender, expanded terminally but not curved downwards or inwards ; a single supramaxilla ; edge of dentaries not reflected outwards, dentaries meeting at their symphysis at an acute angle (Text-fig. 2*c*). Second suborbital with diagonal front border, leaving exposed area above lower limb of preoperculum. Suboperculum not rectangular, anterior and upper borders of the exposed portion of the bone forming an angle greater than 90° (Text-fig. 3*b*). Gillrakers on first arch at least threequarters of the length of the corresponding gill filaments ; outer demibranchs on the first two arches only half the length of the inner demibranchs.

Dorsal rays iii–iv, 13–14, anal rays ii–iii, 19–23, pelvic 8. Scales, 44–45 in lateral series, 17 transversely. Ventral scutes, 17–19 (normally 18) pre-pelvic, 11–12 post-pelvic, total 28–31 (normally 29–30).

A single species recognized, *C. thrissa*.

Konosirus Jordan & Snyder

Konosirus Jordan & Snyder, 1900, *Proc. U. S. nat. Mus.*, **23** : 349. (Type *Chatoessus punctatus* Schlegel.)
Nealosa Herre & Myers, 1931, *Ling. Sci. J.*, No. 10 : 236. (Type *Chatoessus punctatus* Schlegel.) See also Myers, 1931, *Copeia*, No. 1, p. 30.

Indo-Pacific dorosomatid fishes with the last dorsal ray prolonged into a filament. Mouth subterminal ; premaxilla short and in depth intermediate between *Nematalosa* and *Clupanodon* ; maxilla slender, expanded distally and similar to that of *Clupanodon* ; a single supramaxilla ; dentaries with slightly reflected outer edges and meeting at their symphysis at a fairly acute angle (again intermediate between the condition found in *Clupanodon* and *Nematalosa*). Second suborbital with diagonal front border leaving exposed portion above lower limb of preoperculum. Suboperculum not rectangular, anterior and upper borders of the exposed portion of the bone forming an angle greater than 90° (as in *Clupanodon*). Gillrakers on first arch at least threequarters of the length of the corresponding gill filaments ; outer demibranchs of the first two arches at least three quarters of the length of the inner demibranchs (as in *Nematalosa*).

Dorsal rays iii–iv, 15, anal ii–iii, 17, pelvic 8. Ventral scutes 17–20 (normally 18–19) pre-pelvic, 15–16 post-pelvic, total 32–36 (normally 34–35). Scales, 42–46 in lateral series, 17 transversely.

A single species recognized, *K. punctatus*.

7. A Key to the Dorosomatidae of the Indo-Pacific*

I. Last dorsal ray not prolonged into a filament.

A. Maxilla slender, distal end slightly expanded and curved downwards . ***Gonialosa***

i. Depth 2·0–2·5 in length ; 45–47 lateral scales . . . . ***G. modesta***

ii. Depth 2·6–3·2 in length ; 55–65 lateral scales . . . . ***G. manminna***

B. Maxilla straight, thin, tapering terminally . . . . ***Anodontostoma***

i. Dorsal 15 ; 19 transverse scales ; snout little protruded . . ***A. chanpole***

ii. Dorsal 17–18 ; 12–13 transverse scales ; snout well protruded . ***A. chacunda***

II. Last dorsal ray prolonged into a filament.

A. Gillrakers of the first arch at least threequarters of length of corresponding gill filaments ; suboperculum not rectangular, its anterior and upper margins forming an obtuse angle, its posterior margin rounded ; outer edge of dentary not or but very slightly flared.

i. Outer demibranchs on first two gill arches at least threequarters of length of inner demibranchs ; vertebrae 48–51 ; post-pelvic scutes 15–16 ***Konosirus punctatus***

ii. Outer demibranchs on first two gill arches only half length of inner demibranchs ; vertebrae 43 ; post-pelvic scutes 11–12 . . . . ***Clupanodon thrissa***

B. Gillrakers of first arch half or less than half length of corresponding gill filaments ; suboperculum rectangular, its anterior and upper margins forming an approximate right angle ; dentary more or less flared . . . . . . ***Nematalosa***

i. 2nd suborbital covering whole cheek, anterior edge vertical, lower edge horizontal and in contact with preoperculum . . . . . . ***N. nasus***

ii. 2nd suborbital with oblique anterior edge, leaving exposed area above lower limb of preoperculum

a. Post-pelvic scutes 13–16, total ventral scutes 32–34 ; dentary moderately flared ; depth $2\frac{1}{2}$–3 in length.

α Depth $2\frac{1}{2}$–$2\frac{3}{4}$; anal 18–20 . . . . ***N. arabica***

β Depth 3 times in length ; anal 21–23 . . . . ***N. japonicus***

b. Post-pelvic scutes 11–14, total scutes 28–31 ; dentary strongly flared at edges, mouth becoming inferior ; depth 2–$2\frac{4}{5}$ times in length, Australian species.

α 13–14 branched dorsal rays . . . . ***N. come***

β 9–12 branched dorsal rays

† Depth 2–$2\frac{1}{2}$ in length ; pelvics below or immediately in advance of dorsal origin . . . . ***N. erebi***

‡ Depth $2\frac{1}{3}$–$2\frac{4}{5}$ in length ; pelvics below anterior half of dorsal . ***N. horni***

REFERENCES

Blegvad, H. 1944. Fishes of the Iranian Gulf. *Danish Scientific Investigations in Iran*, Pt. 3, pp. 1–247.

Castelnau, F. L. de L. 1873. Contributions to the Ichthyology of Australia. *Proc. zool. acclim. Soc. Vict.*, **2** : 110–158.

Fowler, H. W. 1941. Contributions to the biology of the Philippine Archipelago and adjacent regions. *Bull. U.S. nat. Mus.* 100 (Vol. 13), 1–879.

Herre, A. W. & Myers, G. S. 1931. Fishes from South Eastern China and Hainan. *Ling. Sci. J.*, **10** (2 and 3) : 233–254.

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* Excluding four doubtful Australian species (*N. richardsoni*, *N. elongata*, *N. paracome* and *N. bulleri*) for which there is insufficient published data—see p. 91.

Iwai, T. 1956. The anatomy of the pharyngeal pockets of the Japanese gizzard shad *Konosirus punctatus* (Tem. and Schl.). *Bull. jap. Soc. sci. Fish.*, **22** : 9–11.

Jordan, D. S. & Snyder, J. O. 1900. A list of fishes collected in Japan by Keinosuke Otaki, and by the United States Steamer Albatross, with descriptions of fourteen new species. *Proc. U. S. nat. Mus.*, **23** : 335–380.

Macleay, W. 1880. On the Clupeidae of Australia. *Proc. Linn. Soc. N.S.W.*, **4** : 363–385.

Myers, G. S. 1931. *Nealosa* Herre & Myers equals *Konosirus* Jordan and Snyder (Clupeidae). *Copeia*, No. 1, p. 30.

Regan, C. T. 1917. A revision of the clupeoid fishes of the genera *Pomolobus*, *Brevoortia* and *Dorosoma* and their allies. *Ann. Mag. nat. Hist.* (8) **19** : 297–316.

Roxas, H. A. 1934. A review of the Philippine Isospondylous fishes. *Philipp. J. Sci.*, **55** : 231–295.

Whitley, G. P. 1943. Ichthyological notes and illustrations (Part 2). *Aust. Zool.*, **10** (2) : 168–187.

—— 1948. New sharks and fishes from Western Australia Pt. 4. *Aust. Zool.*, **11** : 259–276.

—— 1956. Ichthyological illustrations. *Proc. R. zool. Soc. N.S.W.* 1955–56, 56–71.

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BY

P. J. P. WHITEHEAD
Department of Zoology, British Museum (Natural History)

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By P. J. P. WHITEHEAD

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INTRODUCTION

The Pantanodontinae, a new subfamily within the oviparous Cyprinodontidae or " killifishes ", was erected by Myers (1955) to accommodate a single genus and species, *Pantanodon podoxys* Myers, based on two small specimens from Dar es Salaam in Tanganyika which entirely lacked jaw teeth. They were briefly described as " Somewhat similar to *Procatopus* but with no teeth in the jaws and ventral rays spiny." No fuller description has since been published.

Recently five more edentulous toothcarps were found in a salt evaporating pool near Gongoni on the Kenya coast, some twenty miles north of Malindi. All are apparently females, mature at less than 20 mm. standard length, and all have normal pelvic fins. They have been compared with a paratype of *P. podoxys*. I must express my gratitude to Prof. G. S. Myers, of Stanford University, California, for lending me this specimen.

The Tanganyika specimen is a male of 30·5 mm. standard length. I can find no difference in meristic characters between this fish and the Kenya specimens, and such proportional differences as exist can be accounted for by its larger size and by sexual dimorphism. However, some male toothcarps are smaller, often considerably smaller, than females of the same species, and although this dimorphism is more marked amongst viviparous than oviparous forms, it is nonetheless surprising to find a male of apparently the same species so much larger. But I do not think this justifies placing the Kenya specimens in a separate species, at least until some Kenya males can be found. The Kenya population was confined to a highly saline pool, whereas the Tanganyika fishes are labelled as found in " swampy land a few miles inland." Thus the Kenya fishes may belong to a runted population living under adverse conditions. Runting is not rare amongst toothcarps.

The Sub-family Pantanodontinae : Relationships

The need for a full revision of the oviparous toothcarps, and especially the African Cyprinodontidae, has become obvious in attempting to establish the relationship of *Pantanodon* to other forms. Some characters used in the following comparisons cut right across the present subfamilial (or tribal) boundaries and yet appear to be equally as " stable " or " important " as characters now used to separate the subfamilies. The two or perhaps three distinct types of maxilla form, the presence of a forked or simple post-temporal, and the fusion of the median hypurals are examples which would seem to merit attention. Since a full revision has not been possible, I have used an existing classification following Myers (1955), and based mainly on earlier work by that author.

Family Cyprinodontidae—oviparous toothcarps
Subfamilies 1. Cyprinodontinae
2. Orestiatinae
3. Fundulinae
4. Rivulinae
5. Procatopodinae (Aplocheilichthyini of Myers, 1931)
6. Pantanodontinae
7. Oryziatinae (Aplocheilini of Myers, 1931)
8. Lamprichthyinae (omitted in Myers, 1955)

(Subfamilies 3–8 were tribes in the subfamily Fundulinae of Myers 1931).

In male *P. podoxys* the anal fin is not modified into an intromittent organ and the genus must be presumed oviparous. This, and the closer affinity shown by *Pantanodon* to African rather than American or Asian genera, seems to reduce the chances that *Pantanodon* is an introduced species.

In attempting to establish the relationship of *Pantanodon* to other oviparous toothcarps, tooth form—a useful key character in separating both genera and subfamilies—obviously cannot be used. Myers (1938) felt that less reliance should be placed on teeth than had been given by Ahl (1924), but nonetheless he was obliged to follow Ahl in separating the genera *Platypanchax*, *Cynopanchax* and *Plataplochilus* solely on the basis of oral dentition. Again, Myers (1931) found little to distinguish his subfamilies Cyprinodontinae and Fundulinae except tooth form (tricuspid teeth in the former).

The absence of jaw teeth in *Pantanodon* is of course remarkable ; indeed it is unique in the whole order Microcyprini. But evidence is given below supporting the hypothesis that degeneration of teeth is but one aspect of a series of modifications arising from specialisation to a purely filter-feeding habit. Such specialisation is suggested by the barely protractile premaxillaries, the modification of the gillrakers into fan structures, the form of the pharyngeal toothpads, and the tightly coiled gut. In all these characters *Pantanodon* departs, often markedly, from the normal cyprinodont pattern. The fact that specialisation has apparently been great enough to eliminate such a stable character as jaw teeth makes it necessary to seek phylogenetic relationships on the basis of characters other than those involved in feeding. Thus the absence of vomerine teeth in an edentulous fish such as *Pantanodon* may not necessarily betoken greater affinities with the subfamilies Fundulinae or Procatopodinae than with the Rivulinae, while a non-protractile premaxilla may well represent an adaptation paralleled by that found in the Oryziatinae.

The two principal characters which can be used to place *Pantanodon* are the fairly high-set pectoral fins and the moderately wide preorbital, and these suggest affinities with the Procatopodinae. The pectorals are not so high as for example in *Aplocheilichthys pelagicus*, but can certainly be considered " high " in comparison with the rivulin *Pachypanchax*. The width of the preorbital region presents a problem since the lacrimal is in fact very much reduced and is narrower even than is found in many Rivulinae. However, the preorbital region as a whole is a little wider than in the Rivulinae. The other characters which would link *Pantanodon* with the Procatopodinae are the absence of vomerine teeth (already commented on) and the absence also of pseudobranchiae. I have been unable to find further characters sufficiently consistent and trenchant to distinguish the subfamilies Procatopodinae and Rivulinae. Thus the presence of a forked or simple post-temporal, and the number of branchiostegal rays, varies within these two groups, as does also the point at which the gill membranes unite, the degree to which the maxillary tip is bound to the lower jaw by skin, and the form of the hypural rays. In cephalic squamation, *Pantanodon* differs from both the Rivulinae and the Procatopodinae. In addition, I know of no other oviparous genus in which the male pelvic fins develop spiny hooks.

Of the procatopodin genera, *Pantanodon* most closely resembles *Hypsopanchax* in the compressed and deep body form. It bears a great resemblance to *A. stuhlmanni* Ahl (which should perhaps be referred to *Hypsopanchax*). However in *Hypsopanchax* the gill membranes are united much further forward. In addition, the predorsal region in *Pantanodon* is shorter (much shorter in the male) than in any genus of the Procatopodinae, the general appearance being much more like the cyprinid than the cyprinodont habitus. The pelvic fins are united by a membrane in *Pantanodon*, similar to the condition in *Procatopus*, but the fin bases are not so far advanced as in the latter genus. There is, however, a strong resemblance between these two genera in body form.

The occurrence of *Pantanodon*, at least in Kenya, near the coast in pools whose salinity often exceeds that of the adjacent sea, makes a link with the Oryziatinae of the Indo-Malayan region and Japan at least a possibility. *Oryzias*, the only genus, has high-set pelvic fins, no vomerine teeth or pseudobranchiae, no parietals (see Ramaswami, 1946), and the premaxillae are non-protractile. In addition, some species are extremely small, females of *O. minutillus* maturing at only 17 mm. (Smith, 1945). But in *Oryzias* the abdomen is not trenchant and the predorsal region is relatively much longer so that dorsal, pelvic and anal fins appear to be set further back.

The fishes of eastern Kenya are part of a general eastern river fauna which is found to the east of the Rift Valleys from the Zambezi to Somaliland. While certain genera (e.g. the cyprinids *Barbus*, *Rasbora*, *Labeo* and *Garra*) occur also in India, the region as a whole does not show any closer affinities with the Indian freshwater fishes than do other regions (e.g. to the west of the Rift Valleys). No genera of Cyprinodontidae are shared with the Indian region, although *Pachypanchax* and *Nothobranchius* are also found in the Seychelles. *Pantanodon* shows little affinity with either of these two rivulins. The only procatopodins which may occur in this eastern river fauna are *Aplocheilichthys stuhlmanni*, but Ahl (1924) does not mention the locality in Tanganyika from which his specimens came, and *A. myoposae* and *A. carlislei* of Natal.

A marine route of entry to the East African coast also suggests affinities with the cyprinodont *Aphanius dispar* (Rüppell). This species occurs for example in reef pools in the Red Sea (Marshall, 1952) and its range extends from N.E. Africa to the Arabian sea coast (Fowler, 1956). But although the body profile is much closer to that of *Pantanodon* than is that of *Oryzias*, the pectoral fins are set much lower, and the preorbital is narrower, the lacrimal overlapping the maxilla.

Thus *Pantanodon* seems to be an isolated form which has become highly specialised in many of those characters of most value in separating the subfamilies of the Cyprinodontidae. The erection of a monotypic subfamily on the basis of trophic adaptation is here felt to be justified because in *Pantanodon* modification has far exceeded subfamilial limits (i.e. supralimital specialisation in the sense of Myers, 1960). At the same time *Pantanodon* shows other marked differences from the Procatopodinae which are unconnected with feeding habits (head squamation, pelvic girdle and rays, narrow lacrimal), but in no case do these serve to link it more closely with the Rivulinae or any other subfamily. *Pantanodon* therefore appears as a highly aberrant form most closely allied to the Procatopodinae but whose inclusion in that subfamily would either destroy the value of the present definition of the subfamily, or so burden it with unique exceptions that as a working description it would become very clumsy. Thus on practical as well as biological grounds it seems more reasonable to separate *Pantanodon* from the Procatopodinae.

Sub-family Pantanodontinae : Diagnosis

Pantanodontinae Myers, 1955, *Tropical Fish Mag.*, March : 7.

Small oviparous toothcarps of the family Cyprinodontidae characterized by the complete absence of jaw teeth, apparently as a result of specialisation to a filter-feeding habit. Similarly, premaxillaries barely if at all protractile, and gut tightly coiled. Gillrakers slender, but able to expand into minute triangular fans.

No vomerine teeth. Pharyngeal bones bearing transverse bars on which rows of fine teeth are set. Pectoral insertion moderately high. Dorsal short, set behind anal origin. Distal part of the maxilla closely bound by skin. Epiplurals simple. Preorbital wide, about half eye diameter. Gill membranes united well behind posterior border of eye. In males; the tips of the second, third and fourth pelvic rays are spiny and hooked.

Habitus. Body strongly compressed and abdominal region deep and trenchant, especially in males.

Genus ***PANTANODON*** Myers, 1955

Diagnosis as for species (see below).

Pantanodon podoxys Myers, 1955

(Text-figs. 1, 2 and 3)

Description based on five females from Kenya[1] (17–21 mm. standard length) and one paratype, a male, 30·5 mm. standard length from near Dar es Salaam, Tanganyika. Skeletal elements are described from two of the Kenya specimens stained in alizarin. In the proportional measurements (in per cent. of standard length) and meristic counts, the first figure given refers to the male paratype, the figures in parenthesis referring to the Kenya specimens.

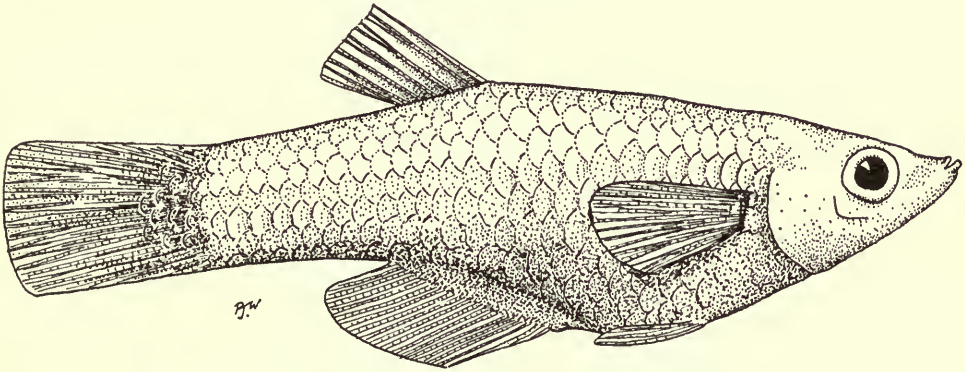

FIG. 1. *Pantanodon podoxys*, female, 21 mm. S.L.

Depth of body 36·5 (27·5–29·5), head length 29·5 (31·5–31·8); eye diameter 8·9 (9·3–9·4), snout length 8·2 (8·6–9·4); predorsal distance 64 (65–69), pre-anal distance 57 (53–54); pectoral length, damaged (22·2 and damaged), pelvic length 13·5 (9·9–10·6); caudal peduncle, length 20·3 (22·5–23·4), depth 18·4 (17·3–17·5), length/depth ratio 1·11 (1·29–1·35).

Body deep, especially in males, strongly compressed, the abdomen trenchant. Snout, in profile acute, equal or just less than eye diameter. Upper lip broad and probably non-protrusible. No jaw teeth. Gill membranes free from isthmus, united behind posterior border of eye. Dorsal about equidistant from snout and tip of caudal rays, its origin over anterior third of anal fin. Pectoral fins set moderately high, the first ray lying on the midpoint of body depth at that point, and just below horizontal through centre of eye; pectoral base inclined forwards at 30° to the vertical. Pelvic fins short, normal in females but tips of 2nd–4th rays modified into

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[1] B.M. (N.H.) No. 1962.4.4.1–2.

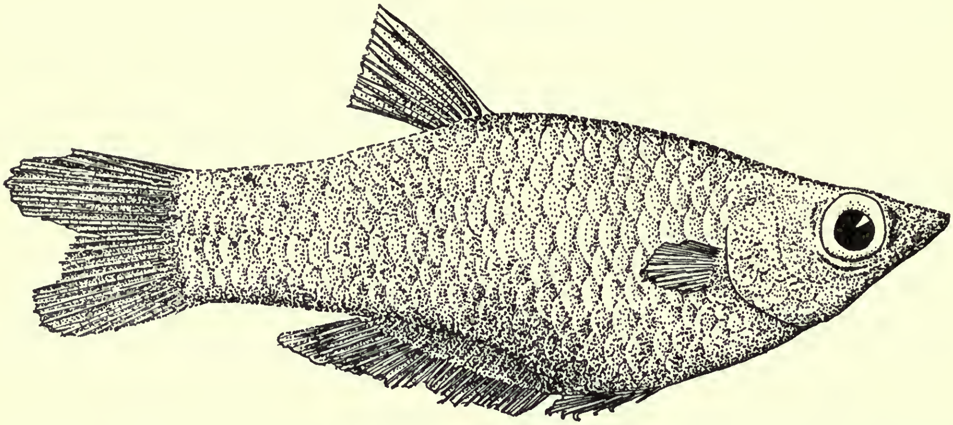

FIG. 2. *Pantanodon podoxys* (male paratype, 30·5 mm. S.L.) Caudal, anal and pectoral fins damaged.

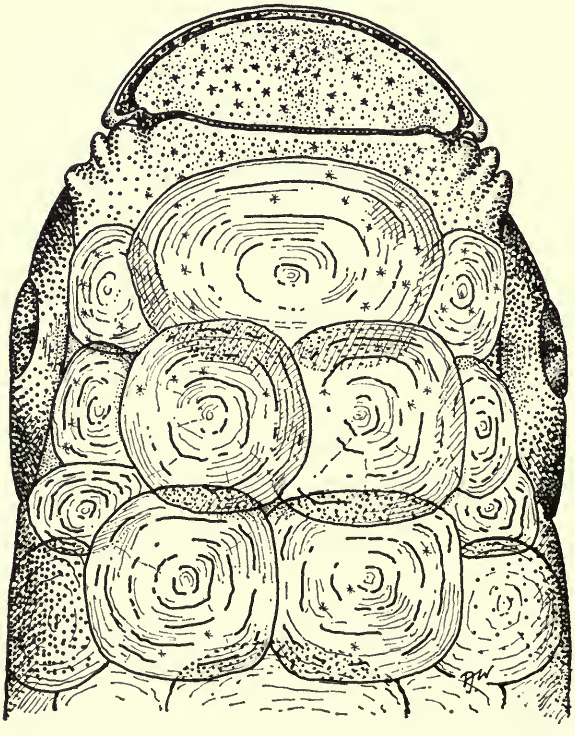

FIG. 3. *Pantanodon podoxys.* Dorsal view of head showing broad upper lip and arrangement of scales.

spiny hooks in males; in both sexes just reaching anal origin. Caudal peduncle deep.

Dorsal i 6–7; anal ii–iii 17–18 (total 20–21), probably not produced posteriorly in either sex; pectoral i 11, rounded in one female but damaged in others; pelvic i 5, the inner edges membranously joined to body; caudal 16–18 branched rays, 10–12 unbranched raylets, the posterior margin of the caudal bluntly round in females (damaged in paratype). About 60 gillrakers on lower part of first arch.

Scales in midlateral series 26–27; 9 scales between pelvic and dorsal origins; 12 round caudal peduncle. Scales sharply bent in ventral midline.

Colour. In life, not recorded; in preserved specimens, a uniform light brown with no distinctive colour markings, but scattered melanophores on head and lip.

Fins hyaline.

Jaw Teeth

These are entirely absent in *Pantanodon.* In sections of the upper and lower jaws of a specimen of 20 mm. S.L. there is no indication even of incipient tooth buds. The very small adult size attained by *Pantanodon,* the rather poor ossification of some cranial elements, the poor development of the head canals of the lateral line system, and the absence of jaw teeth, might all be ascribed to a neotenous condition. But jaw teeth in some toothcarps at least, appear very early indeed in ontogeny. They are present at birth in *Gambusia affinis* (Berner, 1947), are apparently fully formed in *Oryzias curvinotus* of 23 mm. (Nichols & Pope, 1927) and can be seen quite clearly in *Lebistes reticulatus* of only 17 mm.

It is also arguable whether the jaw teeth of *Pantanodon* degenerated under some kind of selection pressure, or whether their incidental loss (through mutation) then stimulated further adaptation to filter-feeding. It is, however, difficult to imagine disadvantages so great that teeth would become a hindrance to be actively selected against. On the other hand, the degeneration of teeth in fishes primarily adapted to seizing and grasping prey would place at great selectional advantage any subsequent adaptations which would assist in filter-feeding.

Pantanodon could perhaps represent an end-point in the reduction of jaw teeth shown by *Hypsopanchax* from the *Aplocheilichthys* condition.

Upper Jaw (Text-figs. 4 and 5)

In *Pantanodon* the upper jaw is barely, if at all, protractile, thus resembling *Oryzias* alone among the Cyprinodontidae. It is, however, difficult to be certain of the degree of protractability of the jaw in such small specimens, especially after preservation in formalin.

Details of the upper jaw mechanism are shown in Text-figs. 4 and 5. The premaxillae are expanded in the midline but do not meet. The descending ramus of the premaxilla is moderately broad and loosely attached distally to the lower jaw so that depression of the latter tends to draw not only the lower ramus but the entire premaxilla forwards very slightly. As a result of this, the upper portions of the premaxilla are raised slightly so that the premaxillae appear to open rather as a flap upwards rather than to be protruded outwards. The maxillae are very slender. The upper ramus lies beneath the expanded portion of the premaxilla and is curved inwards. The descending rami overlap the distal tip of the premaxillae but are curved forwards. Upper and lower rami of the maxilla meet at a weak joint whose shape suggests that it might accommodate the posterior edge of the premaxilla but, owing to the distance between the two, in fact it does not. The lower ramus of the maxilla is produced slightly beyond its junction with the upper ramus and similarly the upper ramus projects beyond this junction also. The rami thus meet edgewise and so a forward movement of the distal tip of the lower ramus can through a twisting action, impart a forward movement also to the upper ramus. In the Microcyprini the mechanical principle involved in the protrusion of the premaxillae differs from that found in other groups (except perhaps the Mugiloidea). Eaton (1935) describes it as the Cyprinodont or twisting type, in which twisting of the lower end of a bow-shaped maxilla imparts a forward thrust to the upper maxillary ramus and

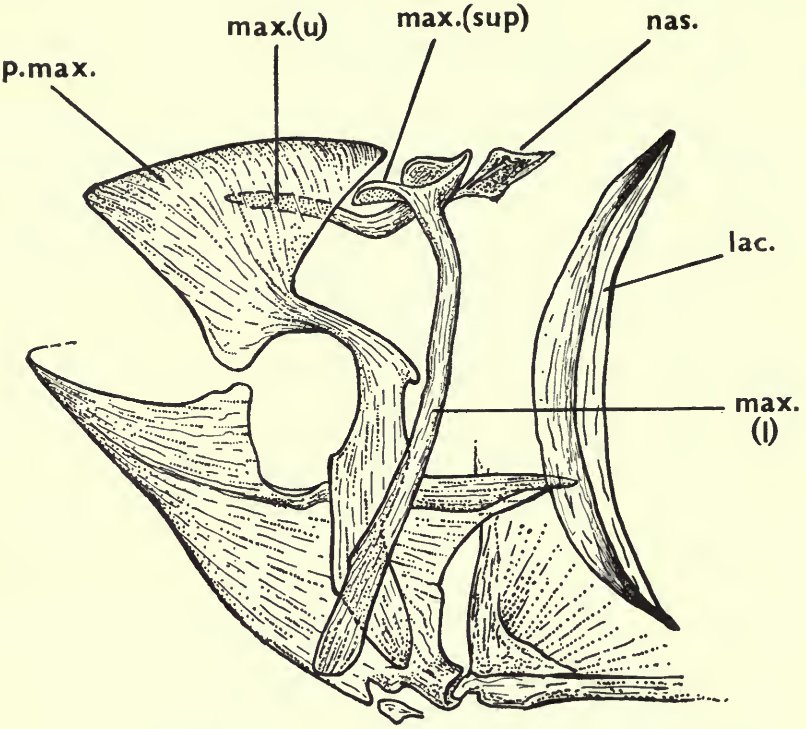

FIG. 4. *Pantanodon podoxys*. Left lateral view of jaw mechanism.

p. max. Premaxilla (upper ramus).
max (*u*). Upper ramus of maxilla (=inferior lobe—see text).
max (*sup*). Superior lobe of upper maxillary ramus.
nas. Nasal.
lac. Lacrimal or preorbital.
max (*l*). Lower ramus of maxilla.

this in turn pushes out the premaxilla. This appears to be mechanically possible in *Pantanodon* but it is hard to say if it is in fact used.

Gosline (1961) has, however, challenged Eaton's view, believing the resemblance between say *Fundulus* and *Mugil* as far as jaw mechanism is concerned to be superficial and secondary. " The maxilla (i.e. in the toothcarps) apparently has very little to do with premaxillary protrusion " (Gosline *loc. cit.*), the distal ends of the premaxilla being membranously attached to the coronoid portion of the lower jaw. He concludes that the Microcyprini have a basically fixed premaxilla (i.e. no descending ramus in *Chologaster* and *Typhlichthys*) from which has later developed the protrusible upper jaw. Loss of protrusibility in *Oryzias* and presumably in *Pantanodon* also, both of which have descending rami, would thus be a reversion to the primitive condition. But in *Pantanodon*, which shows so many structural changes apparently connected with feeding habits, one might expect a more slender lower premaxillary ramus than in fact occurs, although the maxilla in *Pantanodon* is by no means robust.

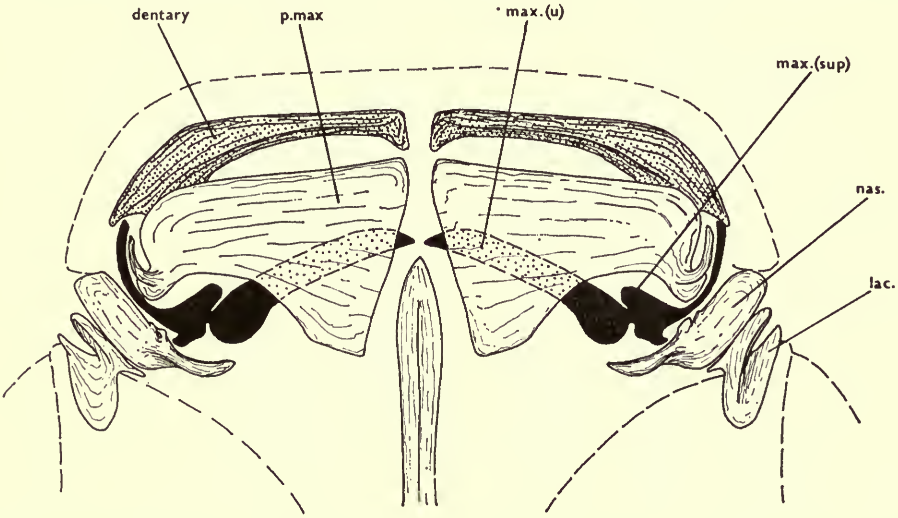

FIG. 5. *Pantanodon podoxys*. Detail of upper jaw structure, dorsal view, from an alizarin stained specimen of 17 mm. S.L. Symbols as in Text-fig. 4.

In *Pantanodon* the upper ramus of the premaxilla is fairly broad. A broad ramus is found in many other species, being perhaps best developed in *Aplocheilus lineatus* (see Ramaswami, 1946). Some species have a rather narrow ramus, e.g. *Micropanchax loati* and *Aplocheilichthys pumilus*.*

As already noted, at the point at which the upper and lower rami of the maxilla meet, there is a tendency for each ramus to be produced beyond the junction, especially in the case of the lower ramus. This latter projection, which may be more or less developed, is here termed the superior lobe, in contrast to the main upper maxillary ramus, which is referred to as the inferior lobe (see Text-fig. 5). Of all the specimens examined, the inferior lobe lies underneath the expanded portion of the premaxilla, except where the premaxilla is too narrow for the two bones to meet. In all but two of the species examined, the superior lobe is no more than a small projection. The exceptions are *A. spilauchena* and *Procatopus nototaenia*, and in these two the superior lobe is greatly developed, reaching and overlying the expanded portion of the premaxilla. This seems to be an intermediate condition, for in those species with narrow upper premaxillary rami, there is only a single maxillary lobe, and from its position it appears to be the superior one ; however, in *M. loati* the superior lobe bears a small, pointed hook on its ventral surface and this may be a poorly developed inferior lobe. Thus there appears to be a gradual transition between forms with only a superior lobe, through those with both lobes well developed, to those in which the superior lobe is small and insignificant. The number of species is, however, too few to show whether this is a line of development which can be related to the evolution of the major groups of oviparous toothcarps.

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* The precise limits of *Aplocheilichthys* and *Micropanchax* still await definition. Here as elsewhere in the text, comparisons are essentially between species and not genera.

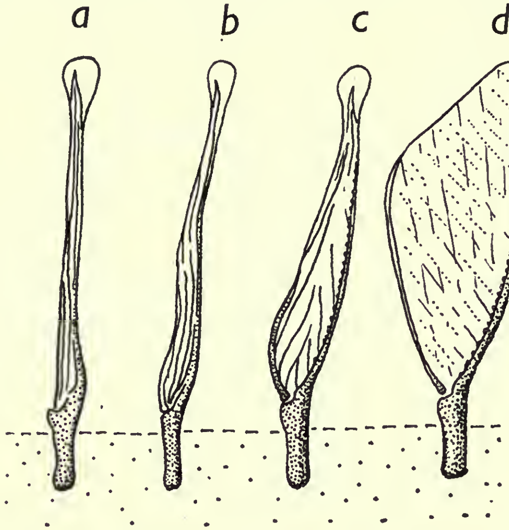

FIG. 6. *Pantanodon podoxys*. Gillrakers : probable stages in the expansion of the external series of gillraker fans. For explanation, see text.

The Gillraker System (Text-figs. 6 and 7)

There are about 50–60 slender gillrakers on the anterior arch. In the specimens measured (15–20 mm. S.L.) the rakers are up to 0·8 mm. in length in the external series and about half this length in the inner series. In addition there is a single series of rakers on the antero-lateral edges of the lower pharyngeal bones ; these are essentially similar in shape to those of the external series on the other arches. Pharyngeal rakers have not been found in other Microcyprini examined (see below), but occur in some cichlids (e.g. *Tilapia*), in the cyprinid *Labeo forskalii*, and also in the Grey Mullet *Mugil cephalus*.

In situ the rakers appear as thin rods, about 100 μ thick and approximately this distance from each other. Each rod has a distinct globular cap and within the rod there is an inner core of bony tissue running the length of the raker and projecting slightly into the globular cap (Text-fig. 6*a*).

When, however, the gillrakers are removed from the arch, mounted on a slide in glycerine and subjected to slight pressure (on the coverslip), they show a more complex structure. The rods then expand into minute triangular fans, their apices being at the point of attachment to the gill arch. The internal and the external fans open in towards each other (i.e. towards the midline of the gill arch (see Text-fig. 7). Each fan has two thickened arms radiating from the apex. In the larger, external fans the subsidiary or smaller arm is distinctly jointed at its junction with the main arm, but this was not seen in the internal raker fans. At the apex of the fan is a small root. The distal edge of the fan is membranous and appears to be derived from the globular cap since the latter disappears in fully expanded fans. Text-fig. 6 shows a series of external raker fans in the process of expanding. In fully expanded fans there are about twenty fine parallel lines running at right angles to the membranous edge but not actually meeting it. Near the apex of the fan these lines tend to converge and form a reticulated pattern. Under very high magnification the lines resemble fine capillaries. If

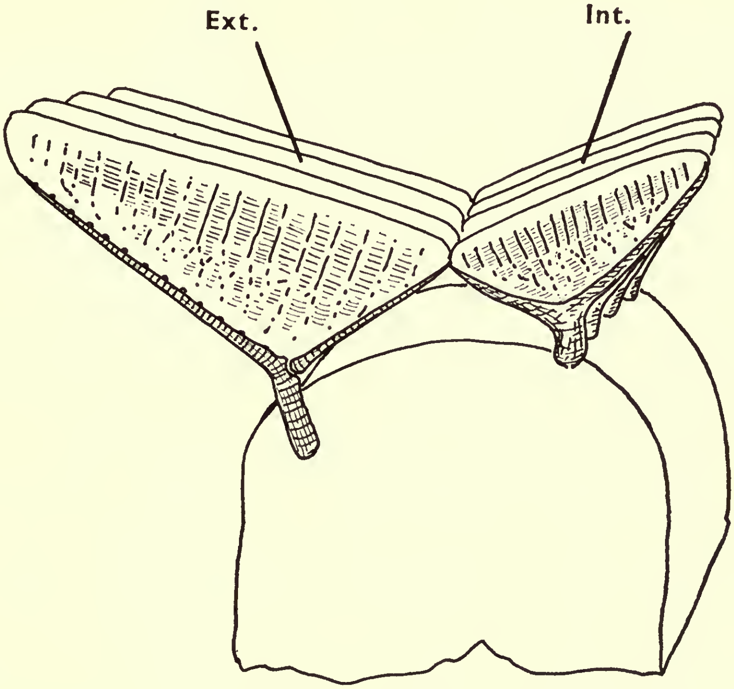

FIG. 7. *Pantanodon podoxys*. Gillrakers: cross section through gill arch showing reconstruction of probable shape and position of inner and outer gillraker fan series when fans are fully expanded. *ext.* external gillrakers. *int.* internal gillrakers.

this is correct, then their distension might well serve to erect the fan. At the same time their alignment also suggests that they offer support for the membrane of the fan. Between these " capillaries " the membrane is marked by a series of transverse lines, extremely fine and close together, which may be lamellae or ridges or even the structural supports of a very fine sieve. Such a sieve would be capable of retaining particles of about 2–3 μ in diameter.

The gillrakers and also the fans when erected, are probably capable of close interdigitation. A discussion of the probable feeding mechanism in *Pantanodon* is given later.

The Pharyngeal bones (Text-fig. 8)

The pharyngeal toothpads also exhibit specialisation towards a microphagous diet.

The lower bones are roughly triangular, pointed anteriorly, rounded posteriorly (see Text-fig. 8*a*). Laterally there are three spines for muscle attachment, the anterior two pointing at right angles to the bone and the posterior spine directed rather postero-laterally. Along the antero-lateral edges of the bones lies a series of gillrakers. The two bones are neither suturally united nor even very closely apposed, resembling the condition found in some cyprinids. The ventral surface of the bones is composed of anterior radiating and posterior reticulated bony ridges. The dorsal surface is made up of a series of ten to thirteen transverse bars each bearing a single row of teeth. Anteriorly the bars are rather weakly joined in the midline, but the posterior two or three bars are free. The lateral edges of the bones are, however, fairly strongly ossified and the lateral tips of the bars are firmly attached to this edge.

The anterior teeth of the lower pharyngeal bones are slender, about 400 μ long, conical and pointed, quite widely spaced (about 300 μ apart) and curved slightly backwards. In the posterior rows, however, the teeth are a little shorter and become so densely packed that there is little or no space between their bases (Text-fig. 8*b*).

The upper pharyngeal bones are essentially similar in structure to the lower bones but are oval in shape (Text-fig. 8*c*). The posterior teeth are about 300 μ in length and about 100 μ apart, tricuspid with expanded crowns, as shown in Text-fig. 8*d*. The cusps show a distinct suture line at their base. In the anterior rows the lateral cusps are progressively lost until the teeth are conical in the anterior two or three rows. Generally, the teeth of the upper pharyngeals are rather more widely spaced than in the lower pads.

The Feeding Mechanism in Pantanodon (Text-figs. 9, 10 and 11)

Divergence of the Pantanodontinae has been almost entirely concerned with trophic adaptation to a filter-feeding habit. Specialisation towards a microphagous diet has apparently involved both the loss and modification of certain structures. Thus jaw teeth have been entirely lost which may preclude the seizure of prey in the normal cyprinodont manner. Secondly, the mouth gape is directed upwards while the premaxillae are more or less fixed. This precludes bottom-feeding and implies that *Pantanodon* must obtain its food from the surface layers. The third specialisation is in the form of the gillrakers. In order to understand their mechanism and possible evolution from the more normal cyprinodont type, comparison was made, first with other Microcyprini, and then with other fishes which use the gillrakers to retain fine particles of food.

Aplocheilichthys pelagicus Worth., the small pelagic cyprinodont from Lake Edward, feeds mainly on small planktonic crustaceans and some insect larvae (Worthington, 1932). In this species the internal gillrakers on the first arch are rod-like and do not expand, but the external rakers of the first arch are long, narrow plates set transversely to the line of the gill arch (Text-fig. 9). Alizarin staining suggests that, like *Pantanodon*, there is an inner and outer ossified support to the raker, but

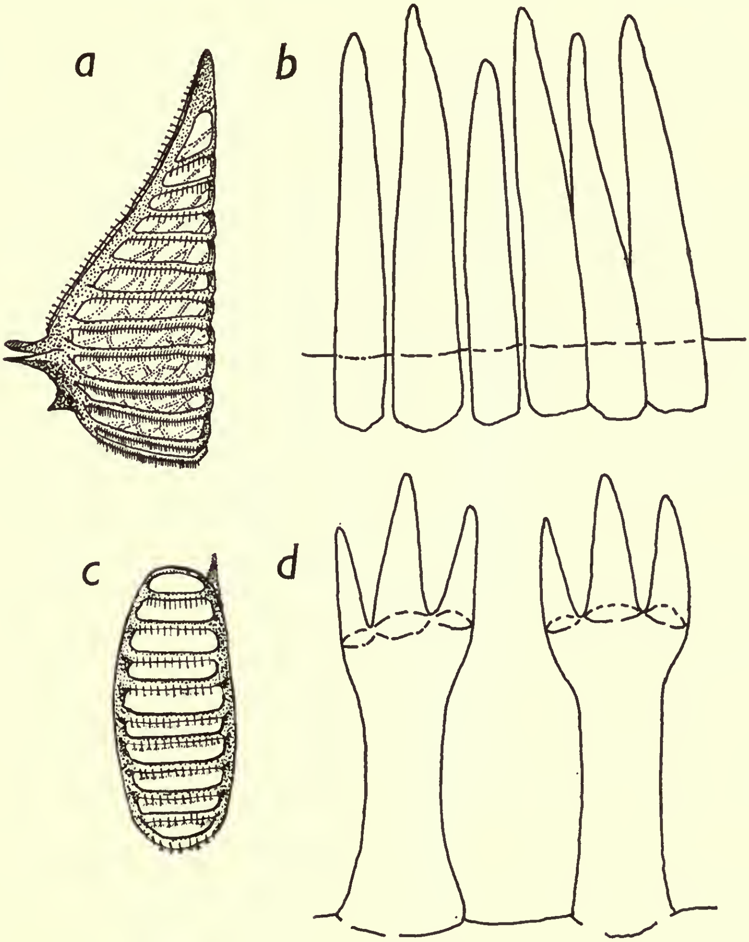

FIG. 8. *Pantanodon podoxys*. Pharyngeal bones and teeth from a specimen 17 mm. S.L.
a. Lower left pharyngeal, dorsal view.
b. Teeth from the posterior rows of the lower pharyngeal.
c. Upper right pharyngeal, ventral view.
d. Tricuspid teeth from posterior rows on upper pharyngeals.

that the lower and middle portions of the plates are also osseous. In the first four or five fans there is a curious tubercle projecting from the inner edge of the fan. The tubercle showed no apparent internal structure and its function is obscure. A narrow membrane runs the length of the inner edge of the fan, and the fans also have one or two fine lines running across their surface, encircling both the tip of the fan and the base of the tubercle, joining in places and leading to the base of the fan. The structure of these lines is not clear ; in places they resemble spirally strengthened capillaries, while elsewhere they could be interpreted as mucus directing or deflecting ridges. In the succeeding arches the external rakers become pointed, and on the fourth arch they are toothed. The large and fairly widely-spaced pharyngeal teeth show that the

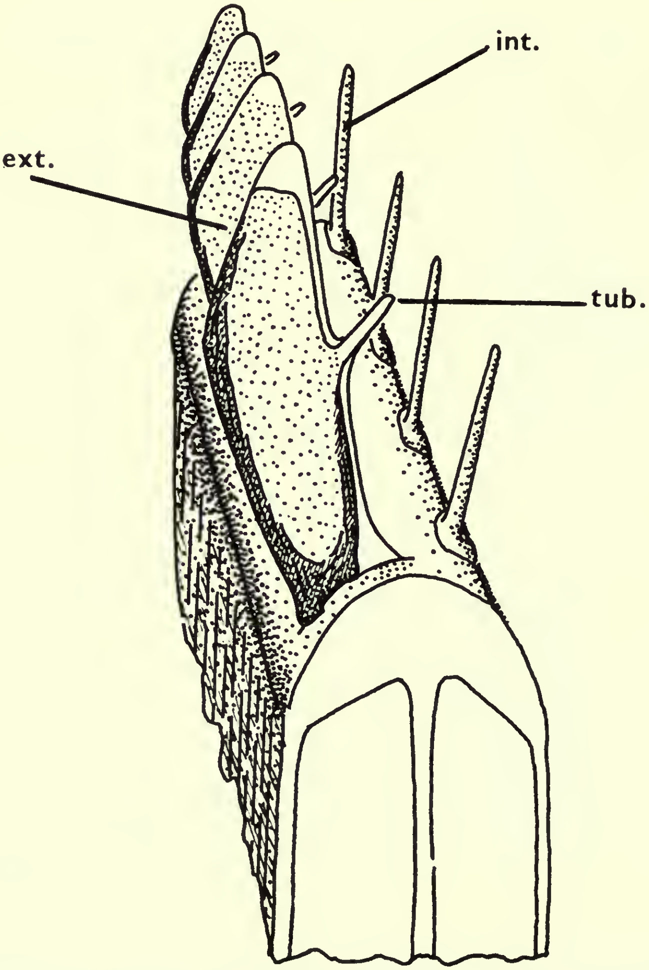

FIG. 9. *Aplocheilichthys pelagicus.* First four gillrakers on 1st gill arch, showing rod-like inner rakers (*int*) and plate-like external rakers (*ext*) which bear a small tubercle (*tub*).

diet is composed of much larger particles than is that of *Pantanodon*, but the plate-like gillrakers on the first arch suggest that smaller particles may also be collected.

Plate-like gillrakers occur in a number of toothcarps, usually only on the first arch, occasionally on the second or on the third, but never in the specimens examined did they extend on to the fourth arch as in *Pantanodon*. *Aplocheilichthys spilauchena*, *A. pumilus*, *Micropanchax loati*, *Pachypanchax playfairii* and an undetermined species of *Mollienesia* all have some development of plate-like gillrakers. In *A. spilauchena* the gillraker plates are not set at right angles to the gill arch but are inclined slightly inwards and backwards, and at the same time the tips of the rakers lean forwards. Such an arrangement may be the case in *Pantanodon* but this could not be seen with the rakers *in situ*.

In many Cyprinodontidae the gillrakers are represented by teeth or tooth-like rakers on some or all the gill arches. The exact homology of these tooth-like rakers is not always clear; some may merely be modified gillrakers, whereas others are probably teeth which have replaced the rakers. Here, all are referred to as " toothed rakers ". Toothed rakers are especially common on the fourth arch and parts of the third, but in some fishes are found also on the second and even the first arch. In most cases the toothed rakers are shield-shaped and lie flat against the surface of the gill arch and their distal edges bear numbers of fine teeth. Those of *Aplocheilus panchax* are shown in Text-fig. 10. Such toothed rakers occur in *Pachypanchax playfairii*, *A. spilauchena* and *Epiplatys sexfasciatus*. In *Aphanius dispar* the rakers of the external series on the first arch are tree-like and branched, while on the fourth arch they are identical in shape to the lower pharyngeal teeth.

In all the specimens examined, those with toothed gillrakers also had a series of minute microgillrakers on the external faces of all but the first arch. A single exception to this was *P. playfairii*. Microgillrakers were not found in any of the species with plate-like gillrakers. The microgillrakers are in many ways homologous with those of certain cichlid fishes (see Gosse, 1955 and Whitehead, 1959), but they are larger and are paired structures (Text-fig. 10). In *E. sexfasciatus* there are no microgillrakers as separate plates, but the base of each raker toothplate has at each corner a series of four or five fine-pointed teeth which evidently serve the same purpose. The disposition of the microgillrakers suggests that they are used to actively clean the raker teeth on the arch immediately in front.

Filter-feeding, or at least the collection and passing backwards of fine particles of food, presents a number of problems. Various methods have been evolved for solving these problems, one of which is the plate system of *Pantanodon*. Perhaps the greatest problem is the need to retain very fine particles by a device which will not clog. In the echiuroid worm *Urechis* this is solved by periodic swallowing of a very fine mucus sieve. In some fishes the cleaning of the sieve system appears to be achieved by the passage of a mucus film to which the particles adhere. The mucus stream must, however, be forced to take a direction different from that of the exhalent stream of water and it seems likely that plate-like gillrakers are at least partly responsible for creating the necessary turbulence for this to happen. In part, also, the shape of the branchial cavity will assist in forcing the mucus back towards the oesophagous, the principle being similar to that of a plankton net. In such a system it would seem that mucus-coated plates would provide a greater collecting surface than would a plain sieve.

A plate system is used by species of *Labeo* (see Text-fig. 11), while the grey mullet *Mugil cephalus* employs a sieve. Comparing these two methods it would seem that the plate system can retain fine particles only in fishes as small as *Pantanodon* (i.e. about 20–30 mm. in length), whereas the sieve system is the more efficient in fishes of 100 mm. and more. *Labeo* is a highly specialized algal grazer, but in spite of interdigitation of the gill plates, there is probably little need for the rakers to retain more than just the ingested algal fragments. In *Mugil cephalus* on the other hand the gillrakers, which are long and very closely set, are joined at their tips and each gillraker bears a double series of minute projections along its length. The projections interdigitate. In a 76 mm. fish, with gillrakers 2·0–2·5 mm. in length, the small projections were 50 μ apart. Each projection, however, bore a series of five to six minute spines along its upper edge, the tips of which were about 5–10 μ apart, and this presumably represents the size of the particles which can be retained. Like *Pantanodon*, *Mugil cephalus* has a series of pharyngeal gillrakers.

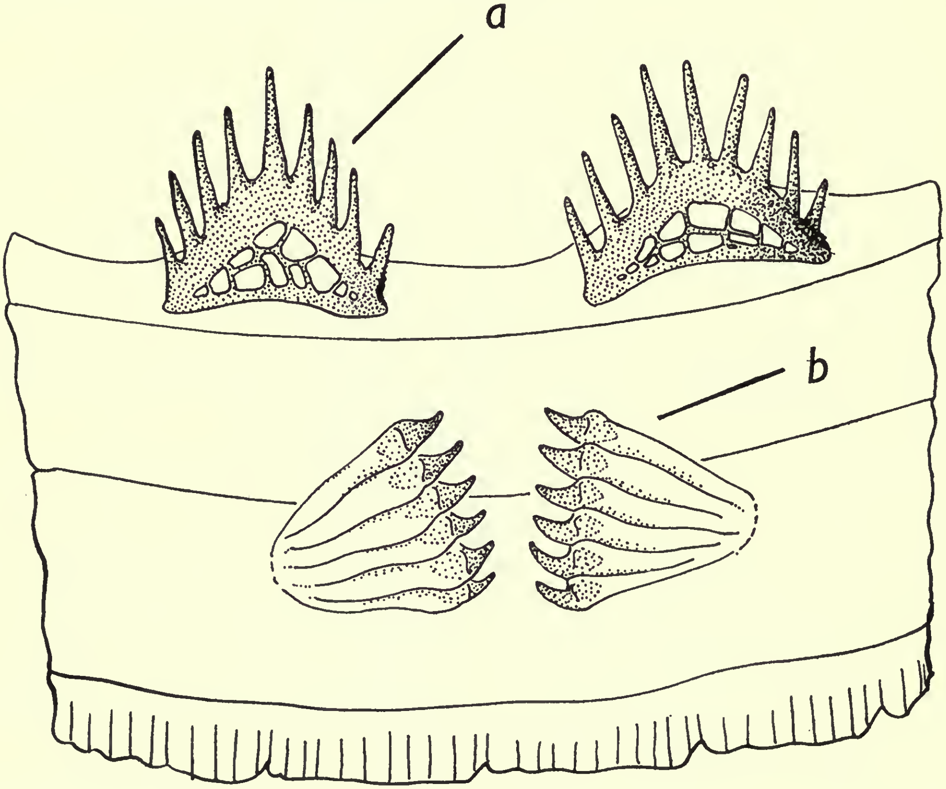

FIG. 10. *Aplocheilus panchax*. External face of second gill arch showing tooth-like gillrakers (*a*) of external series, and position of micro-gillrakers (*b*).

The form of the pharyngeal toothpads in *Pantanodon* differs so greatly from the normal pattern in other cyprinodonts (large, irregularly scattered teeth) that one must regard it as another manifestation of high specialisation to a microphagous diet. It is, however, difficult to imagine why a series of transverse rows of single teeth

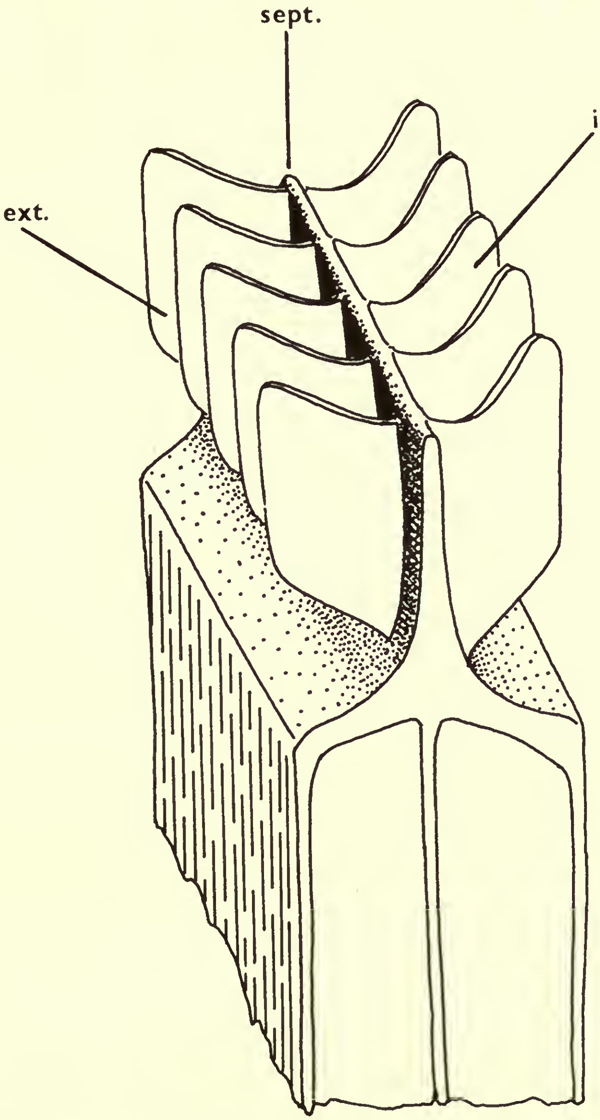

FIG. 11. *Labeo forskalii.* Plate-like gillrakers on the lower part of the 1st gill arch (semi-diagrammatic). Dorso-lateral view looking along gill arch from anterior end.

int. Internal gillraker series.
ext. External gillraker series.
sept. Median septum between gillraker series.

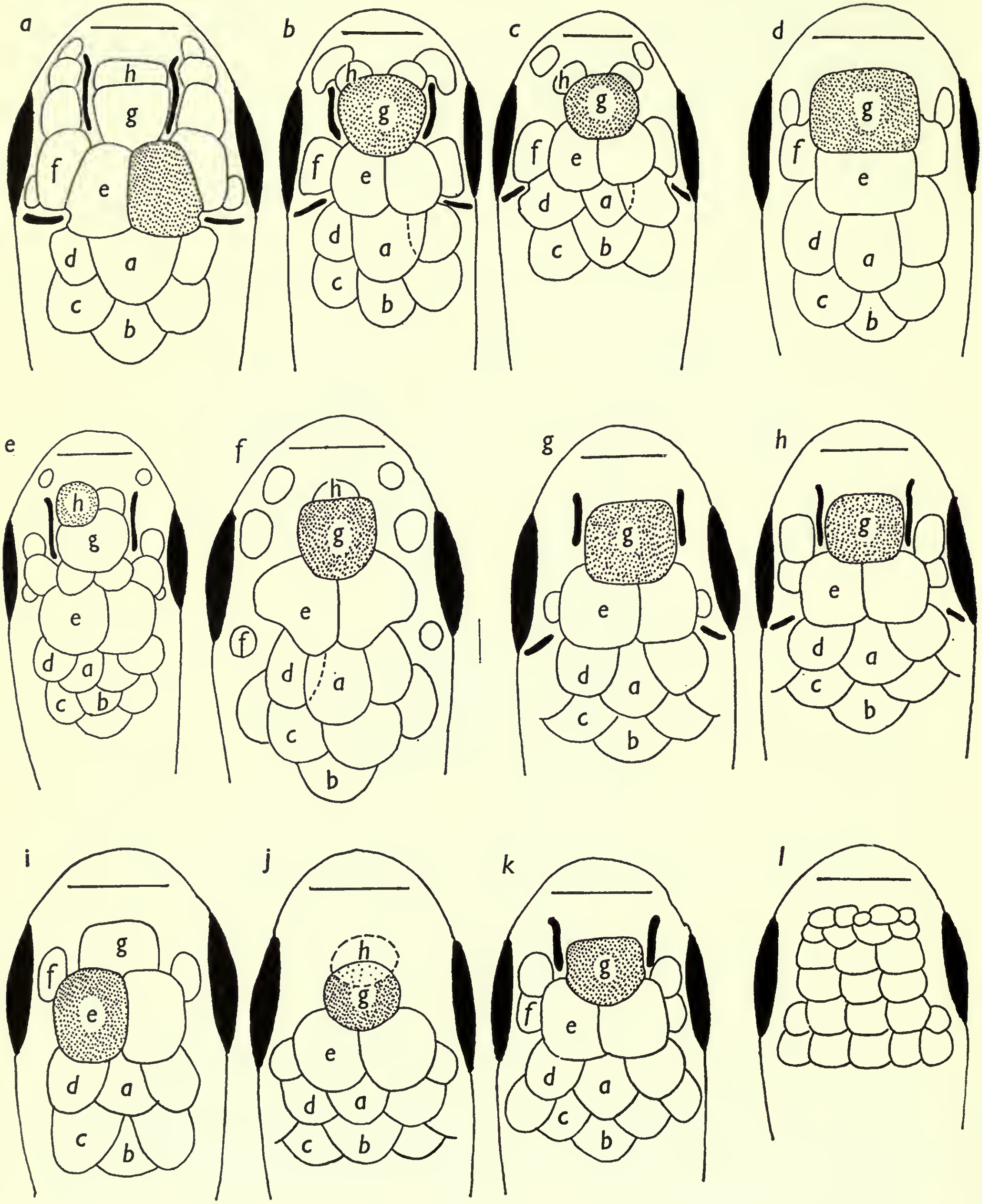
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FIG. 12.

should have arisen rather than a fine but dense mat of irregularly placed teeth, such as is found for example in the microphagous species of *Tilapia*.

In *Tilapia nigra*, which feeds principally on diatoms and is to some extent a filter-feeder, the lower pharyngeal bones are, as in other species, firmly united and cannot move laterally. In *Pantanodon*, however, the lower pharyngeals are only loosely connected, recalling the condition in *Labeo*, in which the bones are ventrally united by transverse muscles. Thus in *Labeo* and *Pantanodon* the lower bones may be able to move to some extent laterally, although in *Labeo* the bones are essentially used for grinding against the horny pad attached to the basi-occipital facet, whereas in *Pantanodon* they appear to act rather as combs.

The final adaptation in *Pantanodon* to a microphagous diet is seen in the very long and coiled gut. The form of winding of the intestine is highly characteristic. It first spirals inwards in a vertical plane, then reverses direction and unwinds in the same plane but on the other side of the peritoneal cavity. Suyehiro (1942) shows an essentially similar kind of winding in the case of *Chaetodon modestus* and *Siganus fuscescens*, but he notes that this form of intestinal winding is unusual. This type of coiling probably allows the maximum length of gut for a given volume of body cavity. The mucosa of the gut is formed into longitudinal zig-zag lines, but it is not known whether such a mucosal pattern can be related to a particular diet or if it holds any taxonomic value.

The Pattern of Cephalic Squamation (Text-figs. 12 and 13)

In a short but useful description of the patterns of scales found on the dorsal surface of the head in many Cyprinodontidae, Hoedeman (1958) showed that the African Rivulini bore less resemblance to the South American forms than they did to the Procatopodinae. Hoedeman considered only a single species of procatopodin, *Aplocheilichthys loati* (= *Micropanchax schoelleri*). I have examined also *Procatopus nototaenia*, *Aplocheilichthys spilauchena*, *A. pumilus*, *A. antinorii* and *A. pelagicus* and confirm Hoedeman's conclusion.

FIG. 12. Cephalic squamation in some Procatopodinae and Rivulinae (semi-diagrammatic). Topmost scale stippled. Scales lettered as explained in text.

a. Aplocheilichthys spilauchena
b. Aplocheilichthys pelagicus
c. Aplocheilichthys pumilus
d. Micropanchax loati
e. Aplocheilichthys antinorii
f. Procatopus nototaenia
g. Aplocheilichthys cameronensis
h. Epiplatys sexfasciatus
i. Pachypanchax playfairii
j. Nothobranchius guentheri (juvenile)
k. Nothobranchius sjoestedti
l. Nothobranchius taeniopygus (large adult).

In order to compare the rather characteristic pattern found in *Pantanodon* with those of other toothcarps, reference must first be made to the system of lettering individual scales employed by Hoedeman (*loc. cit.*). Although this system may occasionally imply a homology which in fact does not exist, nonetheless it is a useful method and one that is used here. The disposition of the head scales is to some extent governed by the position of the head canals. In most Rivulinae and Procatopodinae, there is a prominent pair of canals between the eyes, from the anterior rim of the orbit to about the middle of the orbit (absent, however, in *Pantanodon*); these represent the posterior portion of the supraorbital canal, or pores 2*b*, 3 and 4*a* as designated by Gosline (1949). Immediately posterior to the eye is another part of this canal (pores 4*b*, 5 and 6). From a comparison of my own material with the figures given by Hoedeman and also by Rosen & Mendelson (1960), the basic dorsal head scale pattern in the Cyprinodontidae appears to be reducible to three main elements.

A. Two lateral rows of scales between the anterior part of the supraorbital canal and the orbits themselves, but continuing forwards sometimes to cover the nasals. This lateral series is interrupted by the posterior part of the supraorbital canal. The most posterior scale of this series has been lettered *f*.

B. A median series of scales (single or paired) lying between the anterior parts of the supraorbital canals, reaching forwards to the lip in some cases, and backwards to a line joining the posterior orbital border. This series includes scales *e*, *g*, and *h*.

C. A circle of scales (*b*, *c*, and *d*) immediately posterior to the posterior part of the supraorbital canal. This circle of scales surrounds a single, median scale, *a*.

The pattern of squamation can also be characterized by the particular scale which overlies all the others; in Text-fig. 12, this scale has been stippled, and the fishes said to have a *g*, *d* or *e*-type pattern.

The Procatopodinae resemble the African Rivulinae in having a basic *g*-type pattern, with the *e* scale typically paired. However, in most Procatopodinae examined the *a* scale overlies the two *d* scales; occasionally one *d* may overlap the *a*, but rarely both. With one exception (*Nothobranchius guentheri*) the reverse is true in the African Rivulinae. Small differences such as this are remarkably stable within species and probably do hold a taxonomic weight. Modifications of this basic pattern occur in both subfamilies. In *Micropanchax loati* (Text-fig. 12*d*) the *e* scale is single and not paired as in all other African species examined. Hoedeman notes that *Pachypanchax* has an *e*-type pattern and I have confirmed that this is not merely a single, individual variant (Text-fig. 12*i*). An *e*-type pattern is also found in *Aplocheilichthys spilauchena*, but this appears to be the only other exception to the rule (Text-fig. 12*a*). In *A. antinorii*, possibly because of the small size of the specimens, the normal *g*-type pattern is upset (Text-fig. 12*e*), in the first place by an *h* scale overlying the *g* scale (this may be fortuitous, and does not seem to justify designation of an *h*-type pattern); and in the second place by two pairs of small scales immediately before and after the *e* scales. In Text-fig. 12 I have not labelled the anterior of these pairs since they appear to be too small to qualify as *e* scales. The posterior of these pairs I have considered to represent a paired *a* scale; this interpretation is not entirely satisfactory, but any other would involve an unlikely grouping of the *d*, *c* and *b* scales.

The most striking departure from the normal pattern is found in *Nothobranchius taeniopygus* (Text-fig. 12*l*). Here the scales are arranged in rows as on the body and do not conform to the circular pattern in other genera. A similar situation occurs in the larger specimens of the aberrant *Orestias*, the scales of the head being small and forming a mosaic pattern on the head. Hoedeman's figure for *O. agassiz* is probably derived from a small specimen; thus small specimens of *N. taeniopygus* have the normal circular pattern of scales but this is lost in the larger adults. The figure shown here for *N. sjoestedti* is based on a juvenile; adults may well show the linear arrangement of scales found in *N. taeniopygus*.*

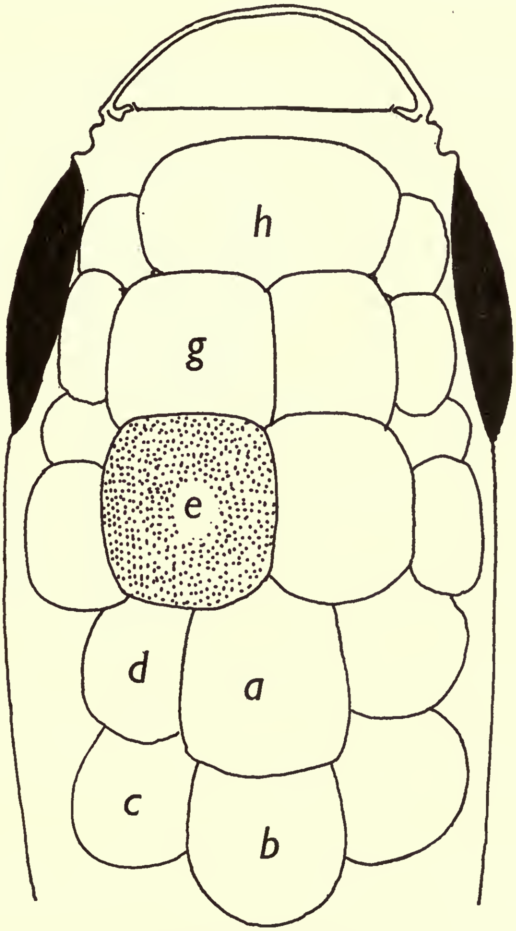

FIG. 13. *Pantanodon podoxys*. Cephalic squamation: topmost scale stippled. Lettering of scales as described in text.

The scale pattern in *Pantanodon* is shown in Text-fig. 13. This differs from the usual pattern in that there are two rows of paired scales anterior to the *a* scale. Although this shows some similarity to the *A. antinorii* pattern, *Pantanodon* cannot be designated a *g*-type genus, and thus it differs from both the Rivulinae and the Procatopodinae. There are two or three possible interpretations ; the one shown in Text-fig. 13, which gives *Pantanodon* an *e*-type pattern, places the *e* scales after and not before the posterior margins of the orbits. To have placed them before would have required a very prominent position indeed for the *d* scales. The text-figure is based on two small specimens from Kenya ; unfortunately the somewhat larger paratype has few head scales.

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* However, Myers (1933) places *sjoestedti* in *Aphyosemion*, and the rather regular pattern of head scales would seem to confirm this.

Whatever interpretation is arrived at, *Pantanodon* evidently differs from both the Rivulinae and the Procatopodinae, although it seems closer to the latter, having the two *d* scales overlain by the *a* scale, and not the reverse (a further reason for considering the *d* scales to be correctly placed in the text-figure).

Clearly, the pattern of cephalic squamation could well prove a useful systematic tool for the Cyprinodontidae provided due regard is paid to the size of the individuals compared. At the same time, the true homology of the scales must be derived from ontogenetic studies.

Head Canal System (Text-fig. 14)

The degree of development of the sensory cephalic canal system has been shown to have systematic value in some toothcarps, at least where closed canals occur (Gosline, 1949). In *Pantanodon* the canals are much reduced and are open (see Text-fig. 14). The infraorbital canal (*C*) is represented by a short preorbital groove with three pores. The supra-orbital canal (*A*) is also much reduced, and is represented by a post-orbital groove containing pores 6 and 7 (possibly also 5) as designated by Gosline (*loc. cit.*). There is an indication of a single pore on the snout, which may represent pore 1 of the supraorbital canal. Between this pore and pore 6 the supra-orbital canal is either discontinued or firmly closed over with bone ; certainly there is no external indication of the usually quite prominent canals between the orbits found in almost all other Procatopodinae and Rivulinae examined, the portion which incorporates pores 2*b*, 3 and 4*a*. The preopercular canal is complete (*B*), and extends forwards to below the anterior border of the eye. Seven pores are visible. There is no mandibular canal developed.

The pore system in *Pantanodon* shows many basic similarities with other genera examined. The absence of the central portion of the supra-orbital canal may perhaps be rare amongst the African forms, but the mandibular canal is often absent (present in *Epiplatys sexfasciatus*).

The Skull

The small size of the specimens and in many places the rather weak ossification of the bones, have made it difficult to compare the shape, extent, or even the presence of some cranial elements. Thus I cannot be certain whether parietals are present or not although they appear not to be. Absence of a parietal would argue affinities with the Oryziatinae since, contrary to Regan (1911), parietals are absent in *Oryzias* (Ramaswami, 1946). But the sutures between the dermal roofing bones of the skull in

Pantanodon can rarely be seen. In general the skull shows no marked departure from the normal procatopodin type as regards shape and proportions, but some small differences can be noted.

The lacrimal (or pre-orbital) in *Pantanodon* is much reduced anteriorly, the bone consisting entirely of the trough-like groove for the pre-orbital canal. In members of the Procatopodinae the preorbital canal is but a small part of the lacrimal, the bone expanding anteriorly and to a greater or lesser extent covering the ventral portions of the descending rami of the maxilla and premaxilla. In *Pantanodon* there is quite a wide space between the lacrimal and the maxilla and premaxilla tips. In the Rivulinae the lacrimal is to some extent expanded dorsally, but quickly tapers ventrally. On the other hand the whole preorbital region in this subfamily seems to be narrow, the anterior edge of the lacrimal again meeting and sometimes overlapping the maxilla and premaxilla. Myers (1931) uses the size of the preorbital in relation to the size of the eye (respectively more or less than half the diameter of the latter) to distinguish the Rivulinae from the Procatopodinae, and says that despite the rather larger eye in some fishes, this character is trenchant when use is made of comparative material. Although the lacrimal is strictly speaking very narrow in *Pantanodon,* I consider that nonetheless it represents a variation on the procatopodin pattern and is not referable to the rivulin type, principally because the preorbital

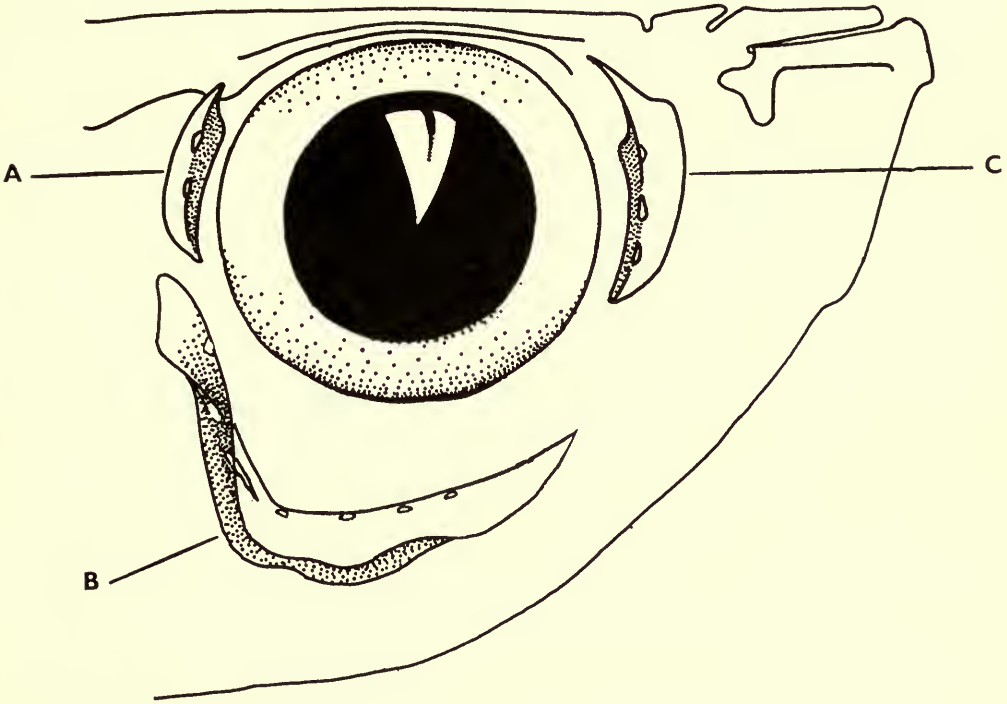

FIG. 14. *Pantanodon podoxys.* Cephalic canal system. A, supra-orbital canal. B, preopercular canal. C, infra-orbital canal.

region *as a whole* (i.e. anterior orbital rim to corner of mouth) is as wide as in the former subfamily and not the latter.

The nasal in *Pantanodon* is also a rather narrow bone, in comparison with members of the Procatopodinae and Rivulinae, in which it often meets and overlaps parts of the maxilla and even the posterior part of the premaxilla.

The post-temporal is forked in *Pantanodon* (see Text-fig. 16), but this cannot be taken as a subfamilial character. Thus it is unforked in *Oryzias* (Ramaswami, 1946); forked in some Rivulinae (e.g. *Epiplatys sexfasciatus*) but not in others (*Aplocheilus panchax, A. lineatus* and *Pachypanchax playfairii*); unforked in some Procatopodinae (e.g. *Aplocheilichthys spilauchena*) but forked in others (*A. pelagicus* for example). The distal end of the main stem is flat and lies on the epiotic. The bifurcation of the post-temporal occurs more proximally in *Pantanodon* compared with other species in which this bone is forked.

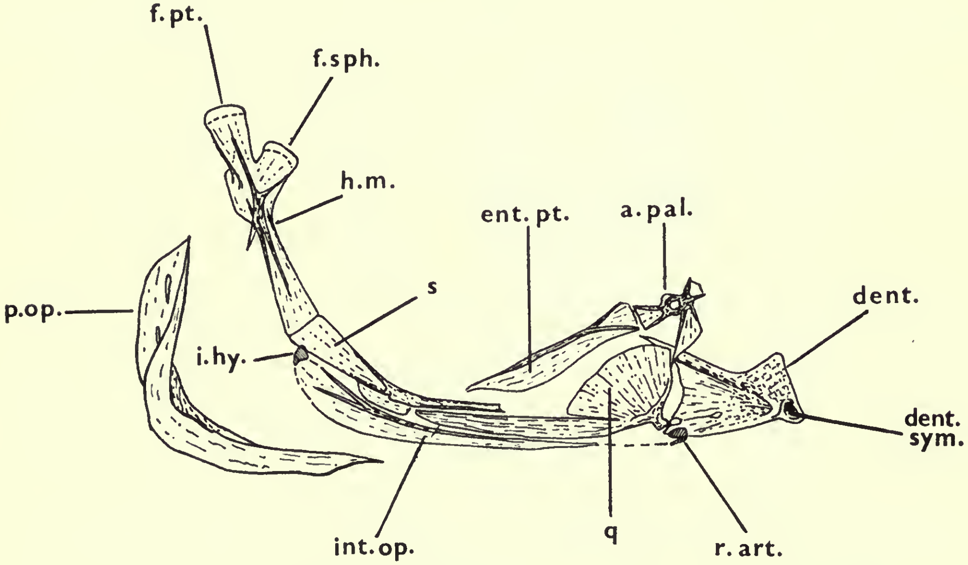

FIG. 15. *Pantanodon podoxys.* Hyomandibular and jaw suspension.

a. pal.	Autopalatine	*h.m.*	Hyomandibular
dent.	Dentary	*i. hy.*	Interhyal
dent. sym.	Cup-shaped symphysis of the dentary	*int. op.*	Interoperculum
		p. op.	Preoperculum
ent. pt.	Entopterygoid	*q.*	Quadrate
f.pt.	Pterotic facet	*r. art.*	Retro-articular
f.sph.	Sphenotic facet	*s.*	Symplectic

The elements in the hyomandibular-jaw suspension series are generally rather weak and resemble those figured for *Oryzias melastigma* by Ramaswami (1946), but the articular facets of the hyomandibular are relatively large and there are two cartilaginous facets and not one (see Text-fig. 15). As in *Oryzias*, the symplectic is narrow and there is no metapterygoid or ectopterygoid; Myers (1931) believed the former entirely absent from the whole suborder Poecilioidea, but Ramaswami (*loc. cit.*) finds a metapterygoid in *Aplocheilus lineatus*. The ventral arm of the quadrate is relatively long. There is a small retroarticular. The junction between the angular and the dentary is not well demarcated. The symphysial surface of the dentary is cup-shaped, and presumably accommodates a ball-joint of cartilage.

In the opercular series, the preoperculum is reduced (rather like the lacrimal) to a curved open groove containing the preopercular canal . The groove is not a surface formation, but is formed in the posterior and ventral edge of the bone, as Tchernavin (1946) has shown to be the case in all other Cyprinodontidae. Other opercular elements scarcely differ from their counterparts in members of the Procatopodinae and the Rivulinae.

Branchiostegal Rays

In *Pantanodon* there are five branchiostegal rays, three attached to the epiphyal and two to the ceratohyal. The number of rays varied between four and six in the other species examined. The number cannot be correlated either with subfamilies or even genera. Thus in the Procatopodinae, *Procatopus nototaenia* has six, *Aplocheilichthys spilauchena* has five, while *A. schoelleri*, *A. pumilus* and *A. pelagicus* have only four; and in the Rivulinae *Epiplatys sexfasciatus*, *Pachypanchax playfairii* and *Aplocheilus panchax* have six, while *A. lineatus* is reported to have only five (Ramaswami, 1946).

Pectoral Arch (Text-fig. 16)

The base of the first pectoral ray is set at about the midline of the depth at that place and on a level with the lower edge of the eye pupil. In comparison with the low-set pectorals of the Rivulinae (*Epiplatys* or *Pachypanchax* for example), that of *Pantanodon* must be considered high, although as Myers (1931) pointed out, the distinction between high and low pectorals is in some cases confusing. The fin base is inclined at about 30° to the vertical.

The pectoral arch is shown in Text-fig. 16. The bifurcation of the post-temporal occurs at the junction of this bone with the tip of the cleithrum, so that the expanded portion of the post-temporal is contained wholly on the cleithrum, and not merely its distal tip, as for example in *Epiplatys*. I have been unable to detect a post-cleithrum in *Pantanodon*; if present, this bone must be extremely small and weakly ossified, as in *Pachypanchax playfairii*. The pectoral radialia are weak and the fourth radial is barely apparent. The coracoid is not keeled ventrally, but has a narrow, more strongly ossified bar running diagonally to its anterior tip. The coracoid foramen is large. The scapula and the upper part of the coracoid are weakly ossified compared with the lower part of the coracoid (suggested by stippling in Text-fig. 16). There are twelve pectoral rays, the first three articulating directly with the edge of the scapula, the remainder with the radials.

The pectoral arch of *Pantanodon* shows no marked specialisation or departure from the general form found in the other genera examined. The distinction between the high-set pectorals of the Procatopodinae and the low-set pectorals of the Rivulinae appears to be rather one of degree than of any structural difference. In the Rivulinae the cleithrum is less steeply inclined while, at least in *Pachypanchax playfairii*, the upper end of the cleithrum is not extended in compensation, but the post-temporal is much longer. As a result, the base of the first pectoral ray is brought on a level with the lower rim of the orbit. In the small Kenya specimens of *Pantanodon* the

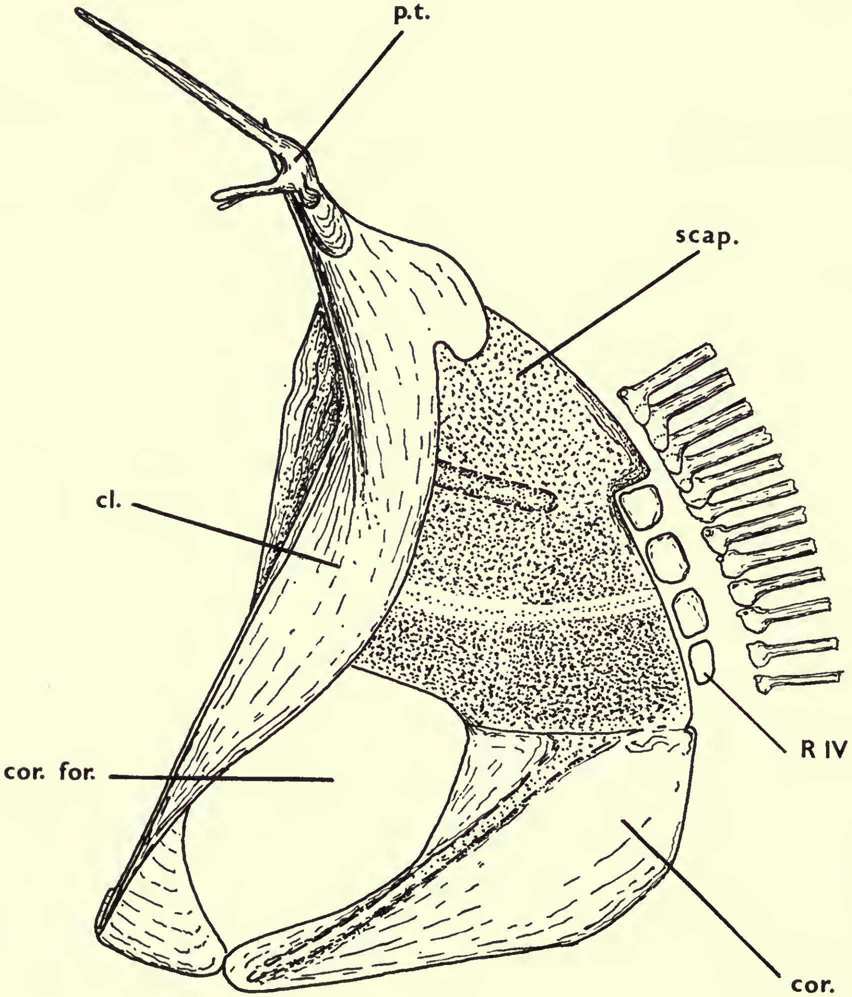

FIG. 16. *Pantanodon podoxys*. Pectoral arch (left, external face). From an alizarin stained specimen 17 mm. S.L.

p.t. Post-temporal	*cor. for.* Coracoid foramen
cl. Cleithrum	*scap.* Scapula
cor. Coracoid	R IV. Fourth radialia

first ray is level with the centre of the eye ; in the larger paratype, it is a little below this, but this may be due to the greater body depth of the paratype.

Pelvic Girdle (Text-figs. 17 and 18)

The pelvic support bones are T-shaped, with a very slender median portion (Text-fig. 18). In five other genera examined (*Procatopus*, *Pachypanchax*, *Aplocheilus*, *Micropanchax* and *Aplocheilichthys*) the median portion is very much broader than this. Judging from these five genera, there seems to be considerable variation in the shape of the two lateral processes of the pelvic support, the inner wings overlapping more or less firmly, and the outer wings in some cases being produced posteriorly, presumably for added support. There are no " splint " bones in *Pantanodon* such as described by Gosline (1961) for *Fundulus majalis* ; but this author notes their absence in another species of *Fundulus*, and the possession of splint bones may not hold much signficance in the Cyprinodontidae.

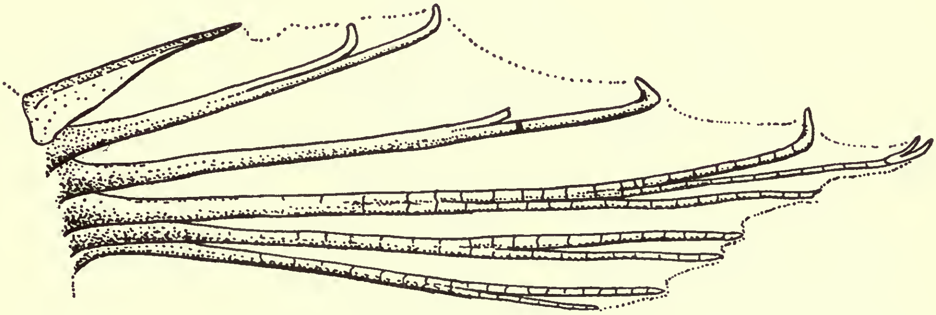

FIG. 17. *Pantanodon podoxys*, male. Left pelvic fin, ventral view, showing hook-shaped tips to the first three branched rays. Second ray unsegmented, but signs of segmentation in third.

In the female specimens of *Pantanodon*, the six pelvic rays are perfectly normal. In the male paratype of *P. podoxys*, however, the tips of the rays are modified (Text-fig. 17). The first short ray is spiny and terminates in a point ; the second and third rays, which are branched (the second without segmentation), have hooked, pointed tips directed laterally ; the fourth and longest ray is clearly segmented, and the two outermost branches have hooked tips (the innermost branch is damaged in all cases) ; the fifth and sixth rays are normal and branched.

A thickened, spiny first pelvic ray, and the hooked tips of the second and third rays, appear to be features which are unique amongst the toothcarps. Since they are confined to the male their function may possibly be concerned with some aspect of reproductive behaviour. The only other case of a thickened spine that I know of is in *Jordanella florida* which has a spinous first dorsal ; here the spine is clearly a double unit (i.e. split longitudinally) whereas in *P. podoxys* it is a single unit.

Axial Skeleton

In the two alizarin preparations of *P. podoxys* there are 29 vertebrae, of which 19 are caudal. Of the precaudal vertebrae, the first is without ribs or epiplurals, the next nine bear ribs, and seven of these also bear simple epiplurals also. The first caudal vertebra has an expanded haemal arch, but this is not found in any of the subsequent vertebrae.

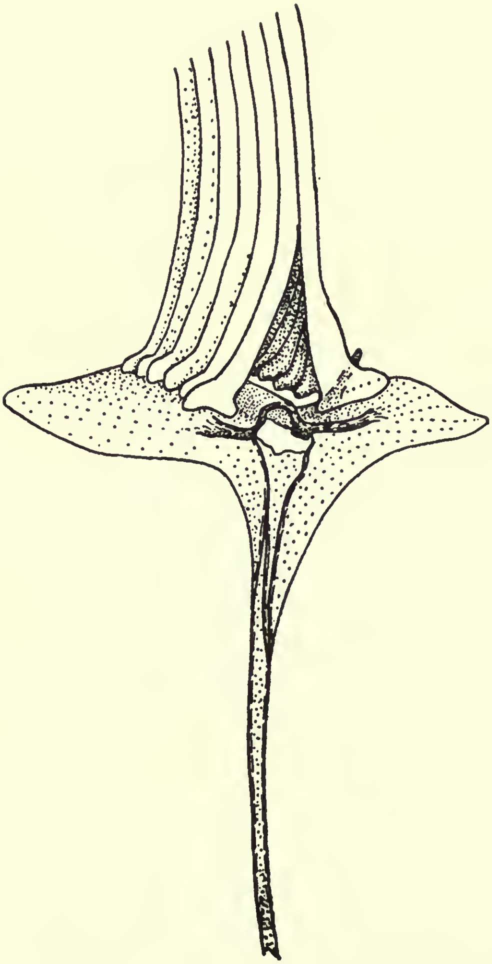

FIG. 18. *Pantanodon podoxys*. Pelvic girdle, right side, ventral view, from a female 17 mm. S.L.

This vertebral formula is little different from that found in other African cyprinodonts, but there seem to be rather more caudal vertebrae in *Pantanodon*. In *Procatopus nototaenia* there are 11–12 + 17 vertebrae, 12 + 16 in *Aplocheilichthys spilauchena*, and 11 + 17 in *Micropanchax loati*. In all of these the first vertebra bears an epiplural (but no rib). In *Pantanodon*, only in the first caudal vertebra is the haemal arch expanded, resembling the condition found in *Procatopus* (one, two or three), *Micropanchax* (one), and *Aplocheilichthys spilauchena* (two); it should be stated, however, that it is not always possible to decide what are elongated parapophyses, and what are short ribs. But *Pantanodon* in no way approaches the condition found in *Epiplatys sexfasciatus* in which up to nine haemal arches are expanded.

The Caudal Skeleton (Text-fig. 19)

The caudal skeleton is shown in Text-fig. 19. The terminology used here is that of Gosline (1960), who preferred the use of " terminal vertebra " instead of " urostyle "

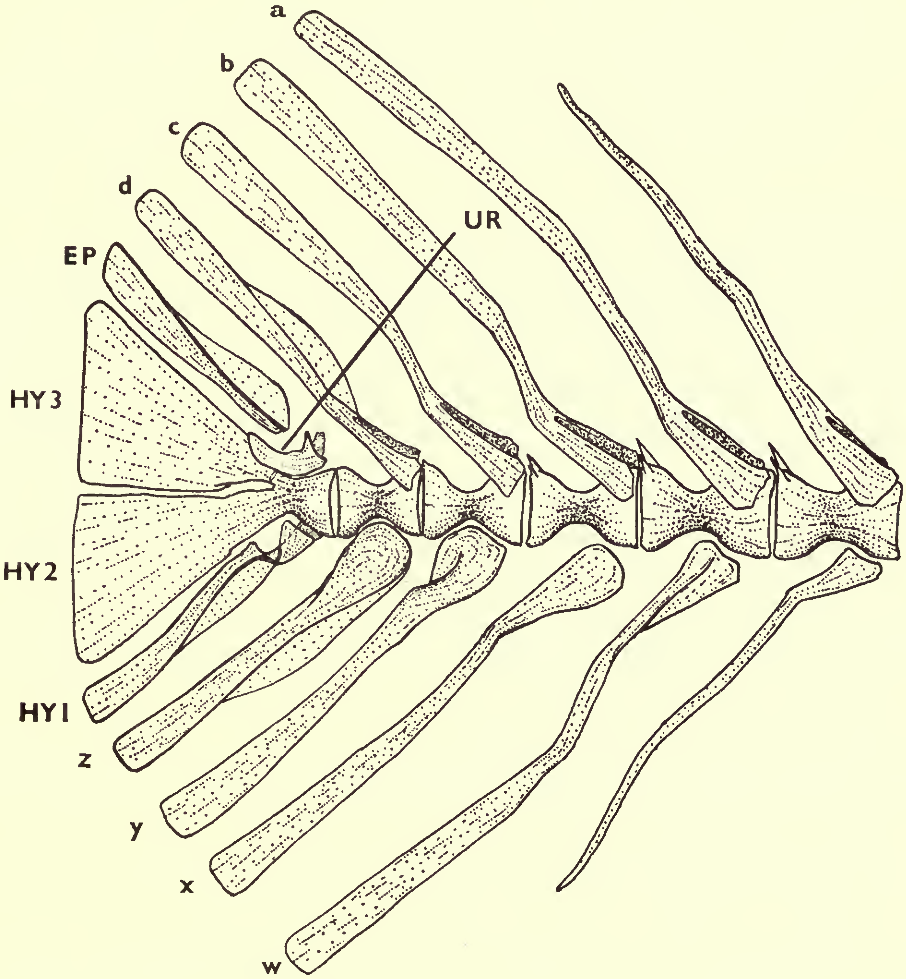

Fig. 19. *Pantanodon podoxys*. Caudal skeleton, from an alizarin stained specimen 17 mm. S.L.
HY 1, 2 and 3. Hypural rays.
EP. Epural.
UR. Uroneural.
a–d. Neural spines directly concerned with caudal support.
w–z. Haemal spines directly concerned with caudal support.

in describing the posteriormost vertebra and the one with which the lowermost and laterally flanged hypural articulates. In *Pantanodon* the terminal vertebra is broadly conical with an upturned end, but there is little indication of the line of demarcation between the posterior border of the terminal vertebra and the base of the median hypurals. There is a small and perhaps paired uroneural (*UR*) lying above the terminal vertebra and overlapping the base of the uppermost hypural. There are three hypurals. The lowest (*Hy* 1 in Text-fig. 19) is a narrow bone which has a slight expansion along its antero-posterior face, and at each side near its base there is a lateral flange with posterolateral muscle attachments. Hypurals 2 and 3 are triangular and similar in shape and size. There is no indication that either is composed of several fused elements. Above hypural 3 there is a single, narrow epural (*EP*), similar in shape to hypural 1 but without an expanded base. The ultimate neural and haemal spines are expanded along their anterior faces into thin wings, and the blades of the last four neural and haemal spines are broader than those of the spines anterior to them (*a–d*, *w–z*). The posterior four spines reach the bases of the caudal rays and raylets, the spines on preterminal vertebra 4 (i.e. spines *a* and *w*) being rather elongated in order to do this.

The separation of hypurals 2 and 3 is well marked in *Pantanodon* and does not appear liable to subsequent fusion in larger fishes, although Hollister (1940) has shown that a tendency for this exists in certain viviparous toothcarps. In a specimen of *Epiplatys sexfasciatus* of 45 mm., however, the division is still complete, whereas in *Procatopus nototaenia* at 28 mm. there is a small split anteriorly, but posteriorly the median hypurals are fused. The hypurals are also split in *Aplocheilichthys spilauchena* and *Apolocheilus panchax*, but no separation of these hypurals was found in *Pachypanchax playfairii* (30 mm.) or in *Aplocheilichthys pelagicus* (40 mm.). Thus this character is not apparently stable amongst the Rivulinae or Procatopodinae, and it cannot be used for subfamilial relationships. Hollister (*loc. cit.*) shows a totally split median hypural in *Mollienesia sphenops*, a partial (anterior) median split in *Gambusia holbrooki* and juveniles of *Lebistes reticulatus*, and completely fused bones in adults of the latter and in *Fundulus bermudae*. In no case, however, does hypural 1 appear to either split or fuse, but in a specimen of *Aplocheilus panchax*, hypural 3 is split—perhaps an individual variant.

In three of the genera examined (*Epiplatys*, *Pachypanchax* and *Aplocheilichthys*) usually only the last three neural and haemal spines are concerned in the support of the caudal rays and raylets ; *Pantanodon* differs from these in its elongated fourth from last haemal and neural spines, which contributes to its deep caudal peduncle. In *Aplocheilichthys spilauchena* also, four spines support the caudal, while in *Aplocheilus panchax* only two neural and three haemal spines are concerned.

Uroneurals are not easy to distinguish in larger alizarin preparations, but they appear to be present also in *Procatopus*, *Aplocheilus* and *Aplocheilichthys*, but could not be seen in *Epiplatys*.

Apart from the small differences mentioned, the caudal skeleton of *Pantanodon* differs little from the other three genera, or indeed from the poeciliids described by Hollister (*loc. cit.*). Although fusion of the hypurals and the fate of the uroneurals may provide evidence of evolutionary progress at ordinal level (Gosline, 1960), the variations in the toothcarps examined probably cannot be placed in phyletic series, but represent small variations on a rather similar general plan. In certain amblyopsoids, however, Gosline (1961) shows a rather different caudal pattern, hypural 1 having apparently lost all basal attachment, and hypural 3 being fused with a post-terminal vertebrae. I have found no post-terminal vertebra in any of the specimens already mentioned, nor any indication that they have become fused during ontogeny.

Pseudobranchiae

In *Pantanodon* there are no pseudobranchiae. Pseudobranchiae are not present in the Procatopodinae (or in the Fundulinae) but are found in the Rivulinae, and in these three subfamilies at least, their presence or absence is coupled with the presence or absence of vomerine teeth. The absence of vomerine teeth in *Pantanodon* may, however, represent a recent specialisation connected with feeding habits.

Habitat

I have no further data for the Tanganyika specimens beyond " in swampy land a few miles inland from Dar es Salaam." The Kenya fishes were caught in a ¼ acre salt-evaporating pool, one of a series built in lowlying, swampy land near enough to the sea to be flooded at high spring tides. Nearby are similar natural pools leading to a mangrove swamp, while inland there is a freshwater swamp and the large Sabaki (Athi) river. The lower Sabaki was intensively studied by the author and the only toothcarps discovered were species which had been introduced for malaria control. The pool in which *Pantanodon* was found contained also juveniles of some marine species, together with a runted population of *Tilapia mossambica*, a species well-known to tolerate saline conditions. The salinity of the pool at the time was approximately 40 parts per mille.

DISCUSSION

All too often in this paper it has been necessary to curtail discussion on the relationship of *Pantanodon* to other oviparous Cyprinodontidae owing to the lack of comparable studies on a particular feature. However, even the limited material on which comparisons have been made has indicated several relatively unexplored paths which should be followed up in a full revision of this section of the toothcarps. But since familial, let alone generic or specific descriptions and definitions, are in many instances inadequate, it has been possible here only to suggest *Pantanodon's* possible affinities, the more so because specialisation in *Pantanodon* has affected several useful key characters. It would seem, however, that *Pantanodon* is most nearly related to the Procatopodinae, although this subfamily is only barely represented in East Africa.

There is no reason to suppose that *Pantanodon* is a primitive form, but rather that it is a highly specialised genus which has evolved beyond the presently defined limits of the Procatopodinae. Neither is it an annectant form between the procatopodins and the rivulins. Zoogeographically, *Pantanodon* may represent a relic of a once widespread fauna common to both the eastern and the western watersheds of Africa. It has been suggested elsewhere (Whitehead in press) that the rivers of the eastern watershed of Africa may contain elements of an archaic fish fauna which became isolated from the fauna of the west prior to the spread (in the west) of the many genera now associated with the Nile-Chad-Niger and Congo systems. But whereas the other cyprinodont genera in eastern Africa do not seem to have diverged greatly, *Pantanodon* does not have a counterpart in the west. It may perhaps have become adapted to a niche filled by other filter-feeders in the faunistically richer waters of the west.

ACKNOWLEDGEMENTS

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REFERENCES

Ahl, E. 1924. Zur Systematik der altweltlichen Zahnkarpfen der Unterfamilie Fundulinae. *Zool. Anz.* **60** : 49–55.

Berner, L. 1947. Le dévelopment dentaire chez *Gambusia affinis* (Baird et Girard). *Bull. Soc. zool. Fr.* **72** : 22–30.

Eaton, T. H. 1935. Evolution of the upper jaw mechanism in teleost fishes. *J. Morph. Philadelphia*, **58** : 157–169.

Fowler, H. W. 1956. *Fishes of the Red Sea and Southern Arabia*, Vol. I. Branchiostomida to Polynemida, Weizmann Science Press of Israel, Jerusalem, 240 pp.

Gosline, W. A. 1949. The sensory canals of the head in some cyprinodont fishes, with particular reference to the genus *Fundulus*. *Occ. Pap. Mus. Zool. Univ. Mich.* **519** : 1–17.

—— 1960. Contributions towards a classification of modern isospondylous fishes. *Bull. Brit. Mus. nat. Hist.* (*Zool.*) **6** (No. 6) : 327–365.

—— 1961. Some osteological features of modern lower teleostean fishes. *Smith Misc. Coll.* **142** (3) : 1–42.

Gosse, J. P. 1955. Disposition speciales de l'appareil branchial des *Tilapia* et *Citharinus*. *Ann. Soc. zool. Belg.* **86** : 303–308.

Hoedeman, J. J. 1958. The frontal scalation pattern in some groups of toothcarps (Pisces-Cyprinodontiformes). *Bull. Aq. Biol.* **1** (No. 3) : 23–28.

Hollister, G. 1940. The caudal skeleton of Bermuda shallow water fishes. IV Order Cyprinodontes : Cyprinodontidae, Poeciliidae. *Zoologica*, **25** (1) : 97–112.

Myers, G. S. 1931. The primary groups of oviparous Cyprinodont fishes. *Stanford Univ. Pub. Biol.* Ser. 6, 7–14.

—— 1933. The genera of Indo-Malayan and African Cyprinodont fishes related to *Panchax* and *Nothobranchius*. *Copeia* : 180–185.

—— 1938. Studies on the genera of Cyprinodont fishes, XIV. *Aplocheilichthys* and its relatives in Africa. *Copeia*, 136–143.

—— 1955. Notes on the classification and names of Cyprinodont fishes. *Tropical Fish Mag.* March : 7.

—— 1960. The endemic fish fauna of Lake Lanao, and the evolution of higher taxonomic categories. *Evolution*, **14** (3) : 323–333.

Nichols, J. T. & Pope, C. H. 1927. The fishes of Hainan. *Bull. Amer. Mus. nat. Hist., New York*, **54** : 321–394.

Ramaswami, L. S. 1946. A comparative account of the skull of *Gambusia*, *Oryzias*, *Aplocheilus* and *Xiphophorus* (Cyprinodontes : Teleostomi). *Spolia zeylan.* **24** (3) : 181–192.

REGAN, C. T. 1911. The osteology and classification of the teleostean fishes of the order Microcyprini. *Ann. Mag. nat. Hist.* (8) **7** : 320–327.

ROSEN, D. E. & MENDELSON, J. R. 1960. The sensory canals of the head in poeciliid fishes (Cyprinodontiformes), with reference to dentitional types. *Copeia*, No. 3, 203–210.

SMITH, H. 1945. The freshwater fishes of Siam, or Thailand. *Bull. U.S. nat. Mus. Washington*, **188** : 1–522.

SUYEHIRO, Y. 1942. A study on the digestive system and feeding habits of fish. *Jap. J. Zool.* **10** (1) : 1–303.

TCHERHAVIN, V. V. 1946. On the lateral line system of some Cyprinodonts (Order Microcyprini). *Ann. Mag. nat. Hist.* (11) **13** : 429–432.

WHITEHEAD, P. J. P. 1959. The feeding mechanism of *Tilapia nigra*. *Nature*, **184** : 1509–1510.

—— 1962. A new species of *Synodontis* (Pisces : Mochocidae) and notes on a mormyrid fish from the eastern rivers of Kenya. *Rev. Zool. Bot. afr.* **65** (1–2) : 97–119.

WORTHINGTON, E. B. 1932. Scientific results of the Cambridge Expedition to the East African Lakes, 1930–31. 2. Fishes other than Cichlidae. *J. Linn. Soc. London*, **38** : 121–134.

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A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES (PISCES, CICHLIDAE)

PART V

BRITISH MUSEUM
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NATURAL HISTORY

P. H. GREENWOOD

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LONDON: 1962

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PART V

BY

P. H. GREENWOOD

Department of Zoology, British Museum (Natural History)

Pp. 139–214 ; *Plate* 1 ; 25 *Text-figs.*

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PART V

BRITISH MUSEUM NATURAL

By P. H. GREENWOOD

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INTRODUCTION

This paper is one of two dealing with the piscivorous *Haplochromis* of Lake Victoria. In this part, I have tried to consider a representative sample of species which cover the different morphological types in this trophic group. A species that I consider to represent a morphological type from which the fish-eating species could have evolved, is also described.

Haplochromis brownae sp. nov.

Text-figs. 1 and 25

Haplochromis stanleyi (part) Boulenger, 1915, *Cat. Afr. Fish.* **3**, 295 (one specimen B.M. (Nat. Hist.) Reg. No. 1909.5.4.28; collected by Bayon in the Sesse Islands; apparently this specimen was not considered by Regan in his revision of 1922).

Paratilapia guiarti (part): Boulenger, 1915, *op. cit.* **3**, 336 (one specimen B.M. (Nat. Hist.) Reg. No. 1906.5.30.354).

Haplochromis guiarti (part): Regan, 1922, *Proc. zool. Soc. London*, 174 (the same specimen as above).

Holotype: A specimen 104·0 mm. S.L. from Entebbe; B.M. Reg. No. 1906.5.30.354.

Description. Based on forty-nine specimens (including the holotype) 72–104 mm. standard length.

Depth of body 32·2–39·8 (mean, M, 35·1) per cent of standard length, length of head 30·2–33·4 (M = 31·6) per cent. Dorsal profile of head straight or slightly concave above the eyes, sloping at about 45°.

Preorbital depth 13·8–19·4 (M = 16·3) per cent of head, least interorbital width 26·0–34·0 (M = 29·8) per cent. Snout as long as broad or very slightly broader, its length 28·0–33·3 (M = 30·8) per cent of head; eye diameter 26·0–31·3 (M = 28·6), depth of cheek 18·9–25·9 (M = 22·7) per cent.

Caudal peduncle length 14·6–20·4 (M = 17·6) per cent of standard length, 1·3–1·8 (mode 1·6) times as long as deep.

Mouth horizontal or slightly oblique, the jaws equal anteriorly, the lips not thickened. Length of lower jaw 38·0–42·9 (M = 40·3) per cent of head, 1·7–2·1 (mode 2·0) times as long as broad. Posterior tip of the maxilla reaching or almost reaching the vertical through the anterior orbital margin.

Gill rakers 9–12 (modal numbers 10 and 11) on the lower part of the first gill arch, the lowermost two to five rakers short and stout, the remainder usually slender (specially in fishes with more than ten rakers) but occasionally stout.

Scales ctenoid; lateral line with 30 (f.1), 31 (f.5), 32 (f.32) or 33 (f.11) scales. Cheek with 2 or 3 imbricating rows. Six or 7 (rarely 8) scales between the lateral line and the dorsal fin origin, 6–8 (modes 7 and 8) between the pectoral and pelvic fin bases.

Fins. Dorsal with 22 (f.1) 24 (f.4), 25 (f.37) or 26 (f.7) rays, comprising 13 (f.1), 14 (f.1) 15 (f.18) or 16 (f.29) spinous and 8 (f.1), 9 (f.24) or 10 (f.24) branched rays. Anal with 11 (f.4), 12 (f.42) or 13 (f.3) rays, comprising 3 spinous and 8–10 branched rays. Caudal truncate, scaled on the basal half only. Pectoral fin from slightly shorter than, to as long as the head, 24·4–33·4 (M = 28·8) per cent of standard length.

Teeth. In most specimens the outer row in both jaws is composed of relatively stout and bicuspid teeth, but in many fishes (irrespective of size) the posterolateral teeth in the upper jaw are unicuspid or tricuspid. In a few specimens there is an admixture of bi- and unicuspid teeth anteriorly in both jaws. There are 50–66 (M = 56) teeth in the upper, outer series.

Teeth in the *inner rows* are tricuspid and arranged in 2 or 3 (rarely 4) series in the upper jaw and 1 or 2 series in the lower jaw.

Osteology. The neurocranium is that of a generalized *Haplochromis.* The supraoccipital crest slopes fairly steeply and is moderately deep ; the ethmoidal region slopes fairly steeply and the vomer is curved ventrally. The preotic part of the skull is 55–58% of the basal length (as measured from the tip of the vomer to the posterior rim of the basioccipital). The lower *pharyngeal* bone is slender, the teeth cuspidate and fine, without markedly enlarged teeth in the median rows. The dentigerous surface is as broad as it is long and there are 34–40 rows (counted antero-posteriorly) of teeth.

Number of vertebrae : 29 (f.2), 30 (f.9) or 31 (f.3), comprising 12 (f.1), 13 (f.4) 14 (f.8) or 15 (f.1) precaudal and 16 (f.8) or 17 (f.6) caudal elements.

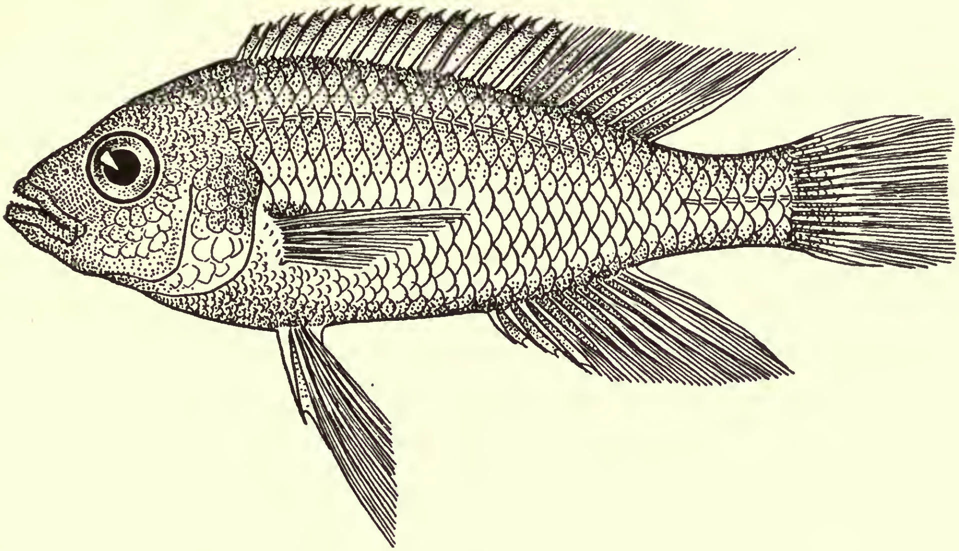

FIG. 1. *Haplochromis brownae* ; natural size. (Drawn by Lavinia Beard.)

Coloration in life. Adult males. Ground colour grey-green dorsally, shading to silver-blue ventrally ; snout dark grey-green. In sexually active fishes a carrot-orange flush develops on the cheek, operculum, flanks and belly ; in such fishes there is also a pronounced lachrymal stripe. Dorsal, caudal and anal fins sooty-grey, the dorsal with three to five horizontal rows of ruddy spots between the spines and rays ; anal ocelli (usually a single row of three or four) orange. Pelvic fins black.

Females have a silver-grey ground coloration (lighter than that of the males) shading to silver ventrally. All fins are hyaline, except the pelvics which are light lemon-yellow. In some individuals there are small orange spots in the position of the anal ocelli in males.

Colour of preserved material. Females. Brownish above, silvery below and on the cheek ; a faint lachrymal stripe is visible as are five transverse bars on the flanks, none of which reaches the ventral profile ; in some specimens there is a short dark, midlateral streak situated above the anal fin. All fins are colourless. In *males* the coloration is more variable, some fishes having a female type coloration (see above) but with a more intense lachrymal stripe and a distinct vertical postorbital bar. All fins, except the pelvics, are hyaline, the dorsal with dusky lappets ; the pelvics are dark laterally but greyish medially.

Other specimens have a similar coloration but the ground colour is darker, the pectoral region sooty and the pelvic fins entirely black. These differences may be associated with the fish's sexual state.

A third varient (undoubtedly attributable to differences in the mode of preservation) almost resembles the live colours. Here the belly, operculum and cheek still retain traces of the carroty flush, the transverse bars are very faint, the lachrymal stripe is intense and the dorsal fin distinctly maculate. The pectoral region is dusky and the pelvic fins are black.

Distribution. Known only from Lake Victoria.

Ecology. Habitat. The species is confined to sandy or shingle beaches where the water is less than thirty feet deep ; such areas are always relatively or completely exposed to wave action. No specimens have been recorded from areas where the substrate is soft.

Food. Twenty of the fifty specimens examined contained ingested material. Of these, three had fed on small fishes (two specimens exclusively so and one on adult termites as well) tentatively identified, in one case, as *Engraulicypris argenteus*, but unidentifiable in the others. Since all three fishes are males the possibility of the fishes having swallowed their own young is eliminated.

The food from the seventeen other fishes is very varied, but it does seem that *H. brownae* is predominantly insectivorous. Larval and pupal Diptera are the commonest foods, but after heavy termite hatches the food can become exclusively winged termites. Other common materials from the gut are macerated fragments of plant tissue and colonial blue-green algae (cf. *Rivularia*). Neither plant shows any signs of digestion. Sand grains and bottom debris are infrequent. Since large numbers of *Rivularia* colonies are often broken away from their substrates after heavy swells, it is possible that the fishes snap up the floating masses as they drift past. Similar concentrations of colonial blue-greens have been found in the guts of other *Haplochromis* whose usual feeding habits do not involve feeding from the bottom. Certainly plants can contribute little to the diet of *Haplochromis brownae* because plant material is apparently indigestible.

Breeding. The species is a female mouth brooder ; the smallest specimen available (72 mm. S.L.) is brooding. Both sexes seem to reach the same maximum adult size.

Affinities. Structurally, and in its diet, *H. brownae* is a generalized lacustrine *Haplochromis*. It differs, however, from the other generalized and insectivorous species of Lake Victoria in having a high number of gill rakers (9–12 *cf.* 6–9) ; in fact very few Victoria species of any structural or trophic group have more than ten rakers. In most other characters *H. brownae* is very similar to *H. melanopus*, another littoral insectivore with similar ecology. The two species do, however, differ in the shape of the lower pharyngeal bone and its dentigerous surface. In *H. melanopus* the toothed area is clearly broader than long, whereas in *H. brownae* the area is equilateral, or almost so. The species also differ markedly in the colours of the breeding male.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.354 (Holotype)	Entebbe	Degen
,, 1909.5.4.28	Sesse Isls.	Bayon
,, 1911.3.3.22	Jinja, Ripon falls	,,
,, 1962.3.2.96–7	Grant Bay	E.A.F.R.O.
,, 1962.3.2.109–113	Beach near Nasu pt.	,,
,, 1962.3.2.114–9	Buka Bay	,,
,, 1962.3.2.120–7	Entebbe Harbour	,,
,, 1962.3.2.128	Beach near Nasu pt.	,,
	Tanganyika	
,, 1962.3.2.76–88	Mwanza, Capri Bay	,,
,, 1962.3.2.89–95	Majita Beach	,,
,, 1962.3.2.98–108	Beach near Majita	,,

Haplochromis guiarti (Pellegrin) 1904

Text-figs. 2 and 25

Tilapia guiarti Pellegrin, 1904, *Bull. Soc. zool. France*, **29**, 186 ; *Idem.*, 1905, *Mem. Soc. zool. France*, **17**, 184, pl. 16, fig. 1.

Paratilapia guiarti (part) : Blgr., 1915, *op. cit.*, **3**, 334 (not the figured specimen).

Paratilapia victoriana (part) : Boulenger, 1915, *op. cit.*, 341 (one specimen, B.M. (Nat. Hist.) Reg. No. 1906.5.30.281).

Haplochromis cinereus (part) : Regan, 1922, *Proc. zool. Soc. London*, 166 (specimen noted above).

Haplochromis guiarti (part) : Regan, 1922, *op. cit.*, 174.

Haplochromis nigroventralis Lohberger, 1929, *Akad. Anz. Wien.*, **66**, 207.

Specimens included in Regan's (1922) synonymy as *Tilapia perrieri* and *Paratilapia longirostris* are no longer considered to be specimens of *H. guiarti*. In his synonymy Regan also included part of *Tilapia pallida* (Boulenger, 1915 *Cat. Afr. Fish.* **3**, 232). Despite an extensive search, I cannot find any specimens referred to this species which Regan might have examined. For this reason I have not included *T. pallida* (part) in my synonymy.

Holotype. A female 114 mm. S.L. (Paris Museum No. 04 × 150) from the Kavirondo Gulf, Kenya.

Description. Based on fifty-five specimens (83–177 mm. S.L.) including the holotype of the species and that of *H. nigriventralis*. All these fishes came from Lake Victoria (see below, p. 147).

Depth of body 27·3–36·5 (M = 32·3) per cent of standard length, length of head 29·5–33·8 (M = 31·4) per cent. Dorsal profile of head slightly curved and sloping at an angle of *ca* 40°–45°.

Preorbital depth 16·3–21·5 (M = 18·3) per cent of head, least interorbital width 23·4–30·2 (M = 27·4) per cent. Snout longer than broad, or, rarely, as long as broad, its length 31·7–37·5 (M = 34·4) per cent of head. Eye diameter shows slight negative allometry with standard length, being 23·6–29·8 (M = 26·5) per cent in fishes < 115 mm. S.L. (N = 16) and 19·7–25·3 (M = 22·0) in larger individuals (N = 39). Depth of cheek shows very slight positive allometry, 20·0–29·0 (M = 25·9) per cent of head for the whole sample.

Caudal peduncle 16·2–20·8 (M = 18·9) of standard length, 1·4–2·0 (mode 1·5) times as long as deep.

Mouth slightly to moderately oblique, the jaws equal anteriorly. Length of lower jaw 39·2–48·2 (M = 44·4) per cent of head, 1·5–2·3 (mode 2·0) times as long as broad. Lips not thickened, the posterior tip of the maxilla not quite reaching the vertical through the anterior orbital margin in most fishes but reaching this point in a few. The dentigerous arm of the premaxilla shows no medial antero-posterior lengthening.

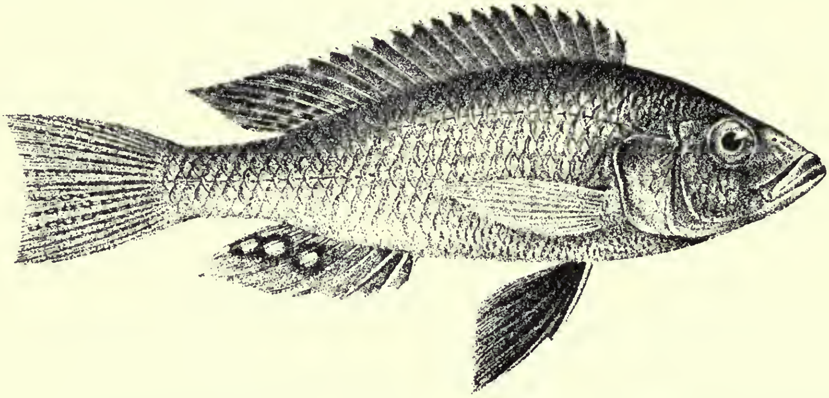

Fig. 2. *Haplochromis guiarti*; about ½ × N.S. (From Boulenger, *Fish. Nile.*)

Gill rakers moderately stout but not stubby; 9–11 (mode 10) on the lower part of the first arch, the lowermost 1–3 rakers reduced.

Scales ctenoid; lateral line with 32 (f.2), 33 (f.26), 34 (f.18), 35 (f.7) or 37 (f.1) scales. Cheek with 3 (less commonly 4 and rarely 2) imbricating rows. Six or 7 (rarely 5, 5½ or 8) scales between the lateral line and the dorsal fin origin; 6 or 7 (rarely 8 or 9) between the pectoral and pelvic fin bases.

Fins. Dorsal with 25 (f.35), 26 (f.19) or 27 (f.1) rays, comprising 15 (f.12), 16 (f.41) or 17 (f.2) spinous and 9 (f.25), 10 (f.29) or 11 (f.1) branched rays. Anal with 11–13 rays, comprising 3 spinous and 8–10 (mode 9) branched rays; in one exceptional specimen there are 4 spines and 9 rays. Caudal truncate, pelvics (particularly in adult males) with the first two branched rays elongated but rarely extending to beyond the first or second branched anal ray (cf. *H. bayoni* where these pelvic rays are greatly produced). Pectoral fin 21·2–27·4 (M = 25·0) per cent of standard length.

Teeth. In fishes <115 mm. S.L. the anterior teeth of the outer row in both jaws are usually unicuspid whilst the lateral teeth are slender and bicuspid. The majority of fishes >115 mm. S.L. have all the outer teeth unicuspid, relatively slender and slightly incurved. However, in several specimens the posterolateral teeth (especially in the upper jaw) are slender and bicuspid or weakly bicuspid. There are 48–74 (M = 62) teeth in the outer row of the upper jaw, the number showing a weak positive correlation with standard length.

In most fishes of all sizes the *inner* teeth are tricuspid but it is not uncommon to find a mixture of tri- and unicuspid teeth, the former predominating. Fishes with the entire inner series composed of unicuspids are rare even amongst specimens >150 mm. S.L. The inner teeth are implanted obliquely and arranged in 3 or 4 (less frequently 2 or 5, rarely 7) rows in the upper jaw and usually in 2 (less commonly 1, 3 or 4) rows in the lower jaw. It seems likely that the number of inner tooth rows is positively correlated with size since there is a tendency for fishes over 125 mm. S.L. to have the higher numbers of rows. Only one fish has seven premaxillary rows (it is a large specimen [170 mm. S.L.] but not the largest) ; the arrangement of these teeth is very irregular and suggests some ontogenetic disturbance.

Osteology. The neurocranium of *H. guiarti* can be considered as a basic type amongst the piscivorous species. Although it shows several characteristics of the " extreme " predator skull (see p. 209) in an early phase of development, it also shows affinity with the generalized *Haplochromis* skull type as seen, for instance, in *H. brownae.* These points are discussed on pages 207–9.

Vertebrae. Thirty or 31, comprising 13 or 14 precaudal and 16–18 caudals. (Based on six specimens.)

Lower pharyngeal bone fine, its dentigerous surface equilateral or somewhat broader than long. The teeth are cuspidate and slender, the most posterior two or three teeth of the two median rows are generally enlarged ; there are 22–28 (mode 26) rows of teeth.

Coloration in life. Adult males. Dorsal surface of head and body intense malachite green shading ventrally to silver. All fins colourless except the pelvics which are black, and the caudal which is dark ; anal ocelli (3 or 4 in a single row) bright orange. *Females* have similar coloration except that the pelvics are light yellow and the anal ocelli are absent or represented by small orange spots. After death the colours change rapidly to dark grey-black above and silver below.

Colour in preserved material. Adult males. Ground colour greenish-grey overlying silver, chest and belly sooty ; a dark lachrymal stripe is generally present. Dorsal fin sooty, the lappets darker and with a small hyaline area between each lappet ; caudal dark on the proximal two-thirds, hyaline distally. Anal fin greyish, the ocelli darker grey ; pelvics black. *Sexually quiescent* males have a female type of coloration but with the transverse bars fainter and the anteroventral part of the body sooty. The dorsal fin is sooty, with black lappets ; the caudal is maculate, the anal hyaline and the pelvics black. *Adult females* are dark grey dorsally, greyish-silver below and becoming silvery-white on the chest and belly. Often there are traces of six transverse bars of lengths varying from short to almost the full depth of the body ; sometimes these bars are connected by a fainter longitudinal stripe. All the fins are hyaline, the caudal often maculate on its proximal half to two-thirds.

Distribution. Lake Victoria and Lake Edward. I have examined three specimens from the latter area. The fishes seem to be referable to *H. guiarti* but I await further material before confirming the occurrence of the species in Lake Edward.

Ecology. Habitat. The species has a lake-wide distribution but is confined to sand or shingle beaches where the water is less than 20 ft. deep. No specimens have been taken over a soft substrate. Information on the distribution and feeding habits of *H. guiarti* given by Graham (1929) must be discounted because several species were confused under this name in his report.

Food. The material found in the alimentary tract of *H. guiarti* may be divided, in order of abundance, into three groups: (1) Fishes (particularly small cichlids) (ii) Insects (particularly winged Termites [Isoptera] and chironomid pupae [Diptera], less frequently larval *Povilla adusta* [the boring may-fly]) (iii) Fragments of phanerogam tissue associated with the colonial blue-green alga *Rivularia.*

Basing the estimate on both frequency of occurrence and on volume, the difference between the amount of fish and the amount of insect food eaten is not great nor is it correlated with the size of the fish. It is difficult to assess the nature of insect-eating habits in this species. At one locality where seine hauls were carried out regularly, it was possible to associate the habit with any high level of insect activity. In this particular case insect-eating might be considered a faculative response to a sudden abundance of a readily available food. The simultaneous occurrence of other species also gorged with the same insects (particularly when the usual diet of these fishes was not primarily insects) seems to indicate that many *Haplochromis* species are " opportunistic " in their feeding habits.

None of the plant matter showed signs of digestion and cannot thus be considered as " food ". As in the case of *H. brownae* (see p. 144) the material may have been accidentally ingested.

In general, the food and feeding habits of *H. guiarti* are similar to those of *H. brownae.* The principal difference lies in the greater proportion of fish eaten by *H. guiarti.*

Breeding. Haplochromis guiarti is a female mouth-brooder; brooding females are found in the same habitat as non-breeding individuals. Sexual maturity is reached at a length of about 100 mm. although some individuals of 110–113 mm. are still immature. There is no marked sexual dimorphism in adult size.

Affinities. Perhaps the nearest living relative of *H. guiarti* is *H. brownae.* The species differ in many respects but the divergence of *H. guiarti* lies in those anatomical (and associated morphometric) characters which we find in a more exaggerated condition amongst the entirely piscivorous predatory species. The resemblance between *H. guiarti* and *H. brownae* is most apparent in young specimens (80–90 mm. S.L.) of the former and adults of the latter species (70–90 mm. S.L.), but even at this size *H. guiarti* is distinguishable on certain characters (longer jaws and snout) which are part of the " predatory species " character complex. However, it is possible that *H. guiarti*, itself still a relatively generalized species amongst the predators, evolved from an *H. brownae*-like stem.

Amongst the larger predatory species, *H. guiarti* is perhaps related to *H. squamulatus*; but the overall resemblance is less than that between *H. guiarti* and *H. brownae.* Another species with about the same degree of relationship as *H. squamulatus* is *H. bayoni* (see p. 152).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.210–2	Entebbe	Degen
,, 1906.5.30.213–5	,,	,,
,, 1906.5.30.220–8	,,	,,
,, 1906.5.30.230	Nsonga	,,
,, 1906.5.30.281	Entebbe	,,
,, 1906.5.30.355–361	Entebbe	,,
,, 1909.5.4.6–7	Sesse Isls.	Bayon
,, 1928.1.25.22	Entebbe	Pitman
,, 1962.3.2.246	Entebbe (Airport Beach)	,,
,, 1962.3.2.240–2	Kagera Port	E.A.F.R.O.
,, 1962.3.2.243–5	Ramafuta Isl. (Buvuma Channel)	,,
,, 1962.3.2.260–3	Entebbe Harbour	,,
,, 1962.3.2.253–9	Bufuka Bay	,,
,, 1962.3.2.264–270	Beach near Nasu point	,,
,, 1962.3.2.248	Karenia (near Jinja)	,,
,, 1962.3.2.271–3	Jinja pier	,,
,, 1962.3.2.274–6	Buka Bay	,,
	Kenya	
Paris Museum 04 × 150 (Holotype)	Kavirondo Gulf	
B.M. (N.H.).—1962.3.2.247	Near Usoma Lighthouse, Kavirondo Gulf	,,
,, 1962.3.2.250–1	Kasingiri Gingo, Kavirondo Gulf	,,
	Tanganyika	
B.M. (N.H.).—1962.3.2.249	Majita Beach	,,
	Lake Victoria, Locality Unknown	
B.M. (N.H.).—1901.6.24.89		Sir H. Johnston
,, 1911.3.3.23		Bayon
,, 1962.3.2.252		E.A.F.R.O.

Haplochromis bayoni (Blgr.) 1909

Text-fig. 3

Paratilapia bayoni (part) Blgr., 1909, *Ann. Mus. Genova* (3), **4**, 304, fig. (the figured specimen only; this specimen is now chosen as the lectotype); *Idem*, 1915, *Cat. Afr. Fish.*, **3**, 337, fig. 227 (figured specimen only).

The syntype on which Regan (1922) based his redescription of the species is no longer considered to be *H. bayoni*.

Lectotype. A male, 147 mm. S.L. (collected in the Sesse Islands by Bayon) i.e. the specimen figured by Boulenger (1909), now in the collections of the Museo Civicio distoria Naturale, Genoa (No. C.E. 12976).

Description. Based on twenty-three fishes (including the lectotype) 82–154 mm. S.L.

Depth of body 27·0–35·3 (M = 32·2) per cent of standard length, length of head 35·0–38·0 (M = 36·3) per cent. Dorsal head profile sloping at an angle of *ca.* 30°–35°, its otherwise straight outline broken anteriorly by the prominence of the premaxillary pedicels.

Preorbital depth 17·7–21·6 (M = 19·6) per cent of head length, least interorbital width 20·8–25·9 (M = 23·2) per cent. Snout longer than broad (1·2–1·3 times), its length 35·3–39·5 (M = 37·5) per cent of head. Eye diameter 17·5–21·9 (M = 20·0) per cent, depth of cheek 23·1–28·1 (M = 25·0) per cent.

Caudal peduncle 14·5–17·2 (M = 16·2) per cent of standard length, 1·1–1·6 (modal range 1·3–1·4) times as long as deep.

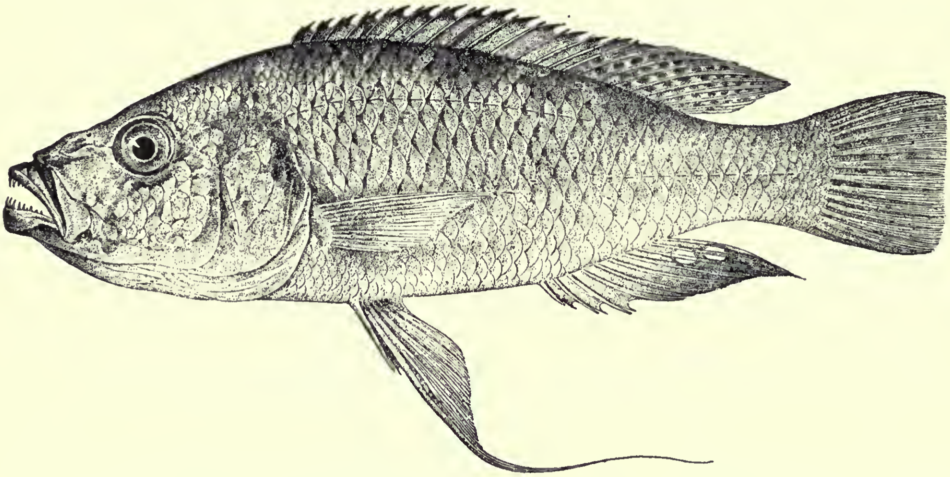

FIG. 3. *Haplochromis bayoni*; lectotype, ·73 × N.S. (From Boulenger, *Ann. Mus. Genova.*)

Mouth slightly oblique, the jaws equal anteriorly or the lower projecting slightly; lower jaw length 42·5–48·0 (M = 45·6) per cent of head, 1·7–2·5 (no definite mode) times as long as deep. Lips slightly thickened, the premaxilla noticeably expanded anteroposteriorly in the midline. Posterior tip of the maxilla not reaching the level of the anterior orbital margin, but generally reaching a point slightly behind the vertical through the posterior tip of the premaxillary pedicels.

Gill rakers usually slender or a mixture of slender and stout, 8–10 (mode 9) on the lower part of the first gill arch, the lowermost 1–3 rakers reduced.

Scales ctenoid; the lateral line with 29 (f.1), 30 (f.1), 31 (f.9), 32 (f.8), 33 (f.3) or 34 (f.1) scales. Cheek with 4 (less frequently 3) series of imbricating scales. Five or 6 (rarely 6½ or 7) scales between the lateral line and the dorsal fin origin, 5 or 6 (less frequently 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.8), 25 (f.13) or 26 (f.1) rays, comprising 14 (f.4), 15 (f.18) or 16 (f.1) spinous and 9 (f.8), 10 (f.13) or 11 (f.2) branched rays. Anal with

12 (mode) or 13 rays, comprising 3 spinous and 9 or 10 branched elements. Caudal truncate. Length of pectoral fin 21·2–28·0 (M = 25·5) per cent of standard length. The pelvic fins have the first unbranched ray greatly produced and filamentous, its tip reaching to at least the third branched anal ray and usually to between the third and sixth rays. In some specimens it reaches to beyond the anal base. Both Boulenger (1911) and Regan (1922) imply that the ray is longer in males than in females but from my sample I can find no clear-cut sexual dimorphism. (Boulenger's remarks are probably attributable to his having another species in his study material). This lack of marked dimorphism is very unusual since in all other Victoria *Haplochromis* the adult male has noticeably longer outer pelvic rays. Indeed, the marked hypertrophy of the pelvic rays in both sexes constitutes one of the most reliable diagnostic characters for *H. bayoni*.

Teeth. In every specimen examined the *outer row* of teeth in both jaws is composed of unicuspid, slightly to moderately curved and relatively stout teeth. There are 34–52 (M = 44) outer teeth in the upper jaw, the number perhaps showing a positive correlation with standard length.

The *inner rows* are also composed of unicuspid teeth, and are implanted obliquely; there are 2 (less commonly 3) series in the upper jaw and 2 (less commonly 1) in the lower.

Osteology. The neurocranium is clearly derived from the *H. guiarti* type but is somewhat more advanced towards the " extreme " predator type of *H. mento* and *H. macrognathus* (see p. 209). Compared with *H. guiarti* the neurocranium has the ethmoid-vomer region more strongly decurved, the slope of the preorbital face less steep (*ca.* 35°), its height less (*ca.* 3 times in basal length *cf.* 2·5 times) and a lower supraoccipital crest. The relative length of the preotic portion of the skull is the same in both species (65% of basal length).

Vertebrae. 28–30, comprising 12–13 precaudal and 16 or 17 caudal elements (4 specimens examined).

Lower pharyngeal bone triangular, its dentigerous surface equilateral. The teeth are relatively coarse and are cuspidate ; the teeth of the two median rows slightly enlarged. There are 18–20 tooth rows.

Coloration. Data on the live colours of *H. bayoni* are not available. In preserved fishes *females and immature males* are greyish-brown above and silver below, sometimes with very faint traces of four short, transverse bars of irregular outline lying midlaterally ; less frequently these bars are joined by an even fainter longitudinal band. All fins are hyaline, the soft dorsal maculate and the proximal two-thirds of the caudal dark with traces of maculae. The only *adult males* available are sexually quiescent and have a coloration like that of the females except for a more intense midlateral stripe and more distinctly maculate dorsal. The pelvics are slightly dusky and there is a single row of three opaque ocelli on the anal fin.

Distribution. Known only from Lake Victoria. Earlier records (Boulenger, 1915) from Lake Kyoga were based on a misidentified specimen.

Ecology. *Habitat*. The species is apparently confined to water less than thirty feet deep and to hard substrates (sand or shingle). The majority of specimens come from exposed sandy beaches but some are from fairly exposed bays where the bottom was of sand or sand overlain by a thin slick of mud. Since only a few of Graham's specimens were preserved, it is impossible to use his records (Graham, 1929) for distributional purposes. If it be assumed that he identified his specimens correctly, then his locality records confirm my idea of the species' distribution.

Food. Information on the feeding habits of *H. bayoni* is scanty. Seven of the fifteen fishes examined (size range 82–154 mm. S.L.; from six different localities) had food in the stomach and/or intestines. In each case the food consisted entirely of finely macerated fish remains, identifiable in four specimens as being small cyprinid fishes (probably *Barbus* sp.). One fish (153 mm. S.L.) had the remains of two cyprinids (*ca.* 35 mm. S.L.) in the stomach and the remains of at least one other fish in the intestines.

Breeding. Nothing is known about the breeding habits of this species. Both sexes reach maturity at a size between 110 and 125 mm. S.L., and both reach the same maximum adult size.

Affinities. The extreme elongation of the first pelvic ray is unique amongst Lake Victoria *Haplochromis* and serves as a ready diagnostic character. On more fundamental structures, particularly the syncranial architecture, *H. bayoni* shows affinity with *H. guiarti* but the relationship is not especially close. In these same characters *H. bayoni* exhibits a further continuation of the trend leading towards the *H. mento*—*H. macrognathus* level of syncranial organization. Phyletically, *H. bayoni* could be considered as an isolated (but by no means aberrant) offshoot from an *H. guiarti*—like stem.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
Genoa Museum, No. C.E. 12976 (Lectotype)	Sesse Isls.	Bayon
B.M. (N.H.)—1962.3.2.160–3	Beach near Hannington Bay	E.A.F.R.O.
,, 1962.3.2.170–1	Beach near Nasu point	,,
,, 1962.3.2.172–4	Entebbe, Airport beach	,,
,, 1962.3.2.175–6	Entebbe, Harbour	,,
,, 1962.3.2.177	Kagera port	,,
	Tanganyika	
,, 1962.3.2.164–8	Majita Beach	,,
	Kenya	
,, 1962.3.2.169	Kavirondo Gulf	,,
	Lake Victoria, Locality Unknown	
,, 1962.3.2.178		,,

Haplochromis serranus (Pfeffer) 1896

Text-figs. 4, 5 and 25

Hemichromis serranus Pfeffer, 1896. *Thierw. D. ost. Afr., Fische*, 23.

Paratilapia prognatha (part): Blgr., 1915, *Cat. Afr. Fish.*, **3**, 333 (specimen B.M. (N.H.), Reg. No. 1906, 5.30.263).

Haplochromis acutirostris Regan, 1922, *Proc. zool. Soc. Lond.*, 180 (the lectotype [and figured specimen] Reg. No. as above).

I do not consider that any of the specimens used by Boulenger (1915) or Regan (1922) to redescribe the species can be referred to *H. serranus*. My concept of *H. serranus* is based on Pfeffer's original description and on supplementary notes and a figure made from the presumed type specimen by Dr. E. Trewavas. The additional material now available agrees more closely with my idea of the type than do Boulenger's and Regan's fishes.

Description. Based on fifty-two specimens, 101–205 mm. S.L. (including the type of *H. acutirostris*).

Depth of body 32·7–39·2 (M = 36·0) per cent of standard length, length of head 34·8–38·7 (M = 36·3) per cent. Dorsal head profile straight or slightly curved, sloping at an angle of 30°–40°, the premaxillary pedicels very prominent.

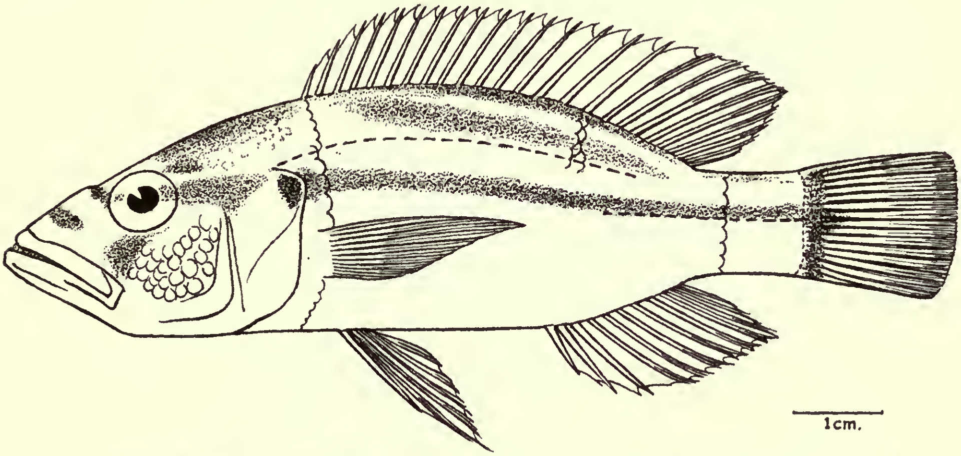

FIG. 4. *Haplochromis serranus*. (Outline drawing of a specimen in the Berlin Museum believed to be the holotype ; made by Dr. E. Trewavas.)

Preorbital depth 14·6–20·0 (M = 17·7) per cent of head, ratio Eye/Preorbital 1·1–1·5, (M = 1·3.) Least interorbital width 20·4–26·8 (M = 23·3) per cent. Snout as long as broad in most specimens, but in some fishes <130 mm. S.L. it is slightly longer than broad ; snout length 30·8–37·0 (M = 34·0) per cent of head, diameter of eye 20·4–26·0 (M = 23·3) per cent, depth of cheek 22·9–31·5 (M = 27·5).

Caudal peduncle length 13·3–19·6 (M = 15·4) per cent of standard length, 1·1–1·5 (mode 1·2) times as long as deep.

Lower jaw moderately oblique, sloping at an angle of 25°–30°, projecting slightly and with a distinct mental bump ; its length 47·7–60·0 (M = 54·3) per cent of head and 1·8–2·5 (mode 2·0) times the breadth. Posterior tip of the maxilla extending to below the eye or to the vertical through the anterior orbital margin in most fishes, but not quite reaching this point in a few.

Gill rakers. Short and stout, 8 or 9 (rarely 7 or 10) on the lower part of the first gill arch, the lowermost one or two rakers reduced.

Scales ctenoid ; lateral line with 30 (f.2), 31 (f.25), 32 (f.18), 33 (f.5) or 34 (f.1) scales, cheek with 4 (less frequently 5, rarely 3 or 6) rows ; 6 or 7 scales between the lateral line and the dorsal fin origin, 7 or 8 (less frequently 9, rarely 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.30), 25 (f.20) or 26 (f.2) rays, comprising 14 (f.2), 15 (f.40) or 16 (f.10) spinous and 8 (f.1), 9 (f.36) or 10 (f.15) branched rays. Anal with 11 (f.6), 12 (f.45) or 13 (f.1) rays, comprising 3 spines and 8–10 branched rays. Pectoral fin length 23·8–33·0 (M = 27·0) per cent of standard length. Caudal truncate (the lower posterior angle somewhat obliquely truncate in a few specimens) scaled on its basal half to two-thirds (rarely). Pelvic fin with the first ray slightly produced and filamentous, proportionately more so in adult males.

Teeth. In all specimens the majority of *outer teeth* are unicuspid but in some fishes <140 mm. S.L. a few bicuspids occur posterolaterally in the upper jaw. The teeth are moderately to strongly curved, the lateral teeth often more so than the anterior ones. There are 44–70 (M = 63) teeth in the upper outer row, the number showing some positive correlation with length in fishes <140 mm. S.L.

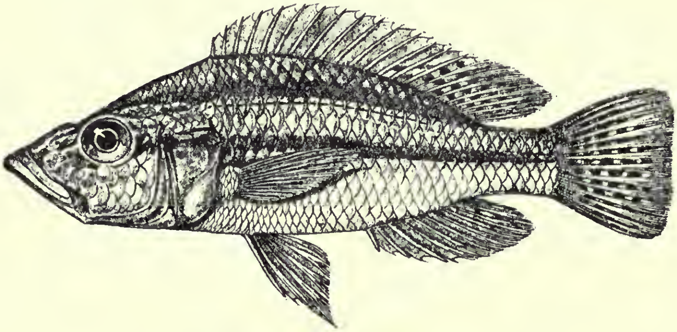

Fig. 5. *Haplochromis serranus*; ·72 × N.S.
(From Regan, *Proc. zool. Soc. Lond.*; the type of *H. acutirostris* Regan.)

All the rows of *inner teeth* (except in some fishes <140 mm. S.L.) are composed of unicuspids.

In the smaller fishes the innermost row (especially in the upper jaw) may be composed of tricuspids or the entire inner series of both jaws may be of tricuspids. The inner teeth are arranged in 2 or 3, rarely 4, rows in the upper jaw and 2, less frequently 1 or 3 rows in the lower jaw.

Osteology. The neurocranium closely resembles that of *H. victorianus* (see p. 157) although the dorsal profile is slightly more curved. It can be considered as a development of the *H. guiarti* type.

Vertebrae. Twenty-eight or 29 (mode 29), comprising 12 (f.1) or 13 (f.6) precaudal and 15 (f.1) or 16 (f.6) caudal elements.

Lower pharyngeal bone triangular, its dentigerous surface very slightly broader than it is long. The teeth are moderately stout and cuspidate, and are arranged in 22–24 rows.

Coloration. The colours of live fishes are unknown.

Preserved material. Adult males. Ground colour light brown, greyish on chest and belly; branchiostegal membrane black or dark grey. In some specimens there is a broad, dark, but faint midlateral band running from behind the operculum to the base of the caudal fin or onto the fin itself, and sometimes an even fainter, interrupted band running slightly below the base of the dorsal fin. The dark lachrymal stripe is very prominent and runs obliquely backwards and downwards from the lower anterior margin of the orbit to the angle of the lower jaw. Dorsal fin brown but with dark streaks between the rays and, in some specimens, with black lappets. Caudal fin darkly maculate. Anal grey-brown, darkest at the base of the spinous part ; ocelli 2–4 in number, greyish and often ill-defined. If there are more than three ocelli, they are arranged in two rows of one and three. Pelvic fins black.

Adult females silvery brown, darker dorsally and apparently without longitudinal bands. All fins are brownish. *Juveniles of both sexes :* ground colour silvery-brown with a broad (sometimes faint) dark midlateral band from the operculum to the basal part of the caudal fin ; lachrymal stripe, if visible, very faint. All fins are greyish, often with traces of maculae on the soft part of the dorsal.

Ecology. Habitat. Most records of *H. serranus* are from sheltered bays and gulfs where the bottom is of soft, organic mud and the depth of water less than 25 feet. A few specimens came from exposed habitats and were caught over sand or shingle, but again the water did not exceed 25 feet in depth. It should be noted that all the latter localities are near muddy areas. No locality is more than half a mile from the shore.

Food. The food of fishes in the size range 100–205 mm. S.L. is exclusively fish and predominantly *Haplochromis* ; no other genus could be identified in the very macerated gut contents of the thirty specimens examined. Some food was, however, too finely divided to even hazard an identification.

Breeding. No information is available on the breeding habits of *H. serranus.* Most individuals <140 mm. S.L. are immature, but one female of 118 mm. S.L. shows early stages of oogenesis. Males and females reach the same adult size.

Distribution. Lake Victoria.

Affinities. Haplochromis serranus is closely related to *H. victorianus* and *H. nyanzae*, the three species apparently forming a species group amongst the larger predatory *Haplochromis* of Lake Victoria. In turn, this group is related to *H. spekii* and the relationship will be discussed in another paper. The differences distinguishing *H. serranus* from *H. nyanzae* are outlined on p. 161 ; from *H. victorianus*, it differs in its more oblique and longer lower jaw (47·4–60·0, M = 54·3 per cent of head *cf.* 44·0–51·8, M = 47·1 per cent), shorter pectoral fin (23·8–33·0, M = 27·0 per cent of standard length *cf.* 26·2–32·7, M = 30·4 per cent) and in having fewer teeth in the outer row of the upper jaw (44–70, M = 63, *cf.* 67–86 M = 74).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.)—1906.5.30.263 (Type of *H. acutirostris*)	Bunjako	Degen
,, 1962.3.2.27–36	Pilkington Bay	E.A.F.R.O.
,, 1962.3.2.37–51	Ekunu Bay	,,

Museum and Reg. No.	Locality	Collector
	Uganda (*continued*)	
B.M. (N.H.).—1962.3.2.52–3	Bukafu Bay	E.A.F.R.O.
,, 1962.3.2.54–5	Jinja pier	,,
,, 1962.3.2.56–7	Karenia (near Jinja)	,,
,, 1962.3.2.61–3	Pilkington Bay	,,
,, 1962.3.2.74–5	Williams Bay	,,
,, 1962.3.2.58	Ramafuta Isl.	,,
	Kenya	
,, 1962.3.2.26	Rusinga Isl.	,,
,, 1962.3.2.60	Naia Bay	,,
	Tanganyika	
,, 1962.3.2.59	Ihogororo	,,

Haplochromis victorianus (Pellegrin) 1904

Plate I

Paratilapia victoriana Pellegrin, 1904, *Bull. Soc. zool. France*, **29**, 185 ; *Idem*, 1905, *Mem. Soc. zool. France*, **17**, 182, pl. 17, fig. 3.

Pelmatochromis spekii (part) Blgr., 1906, *Ann. Mag. nat. Hist.* (7), **17**, 440 ; *Idem*, 1915, *Cat. Afr. Fish.*, **3**, 416 (one of the types, B.M. (N.H.) Reg. No. 1906.5.30.300).

Regan (1922) tentatively included *Paratilapia victoriana* in the synonymy of *Haplochromis nubilus*. I have examined the types of both species and can find nothing to substantiate this arrangement ; indeed, the two species are only distantly related. None of the specimens identified by Boulenger (1915) as *P. victoriana* can be referred to Pellegrin's species.

Holotype. A fish 120 mm. S.L. (Paris Museum Reg. No. 04 × 148) from Kavirondo Bay, Kenya.

Description. Based on twenty specimens 117–166 mm. S.L., including the holotype.

Depth of body 33·4–41·3 (M = 37·3) per cent of standard length, length of head 33·5–36·0 (M = 34·8) per cent. Dorsal profile of head usually straight (but sometimes with a slight concavity due to more prominent premaxillary pedicels), sloping at *ca.* 35°–45°.

Preorbital depth 17·9–20·5 (M = 19·2) per cent of head, ratio Eye/Preorbital 1·1–1·3 (mean 1·2), least interorbital width 21·5–24·5 (M = 22·6) per cent. Snout length 31·8–36·0. (M = 34·1) per cent of head, equal to its width ; diameter of eye 21·7–25·5 (M = 23·6), depth of cheek 22·5–26·2 (M = 24·6) per cent.

Caudal peduncle 13·5–19·6 (M = 17·1) per cent of standard length, 1·1–1·8 (mode 1·5) times as long as deep.

Lower jaw horizontal or slightly oblique, anteriorly equal to the upper or projecting slightly, its length 44·0–51·8 (M = 47·1) per cent of head, 1·6–2·2 (modal range 1·8–2·0) as long as broad ; there is always a well-developed mental prominence at the symphysis. The posterior tip of the maxilla reaches the vertical through the anterior orbital margin, or somewhat more posteriorly, in most specimens but does not reach the orbit in a few fishes.

Gill rakers short and moderately stout, 8 or 9 on the lower part of the first gill arch, the lowermost 1–3 rakers reduced.

Scales ctenoid, lateral line with 31 (f.3), 32 (f.6), 33 (f.9) or 34 (f.2) scales, cheek with 3 or 4 series. Six to 8 scales between the lateral line and the dorsal fin origin, 7 or 8 (rarely 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.1), 25 (f.16), or 26 (f.3) rays, comprising 15 (f.4), 16 (f.14) or 17 (f.2) spinous and 9 (f.16) or 10 (f.4) branched rays. Anal with 11 (f.1), 12 (f.16) or 13 (f.3) rays comprising 3 spines and 8 (f.1), 9 (f.16) or 10 (f.3) branched rays. Caudal fin truncate, scaled on its basal half (rarely two-thirds). Pectoral 26·2–32·7 (M = 30·4) per cent of standard length. First pelvic ray slightly produced and filamentous in both sexes (an unusual feature).

Teeth. In fishes less than 125 mm. S.L., the *outer teeth* in both jaws are mostly bicuspids, but some may be weakly so ; fishes between 125 mm. and 130 mm. S.L. show an admixture of unicuspids and weakly bicuspids, or the unicuspids may predominate ; all fishes >135 mm. S.L. have only unicuspid teeth in this series. In all specimens the teeth are relatively slender and slightly curved. There are 64–86 (M = 74) in the outer row of the upper jaw.

The inner teeth are arranged in two or three rows in each jaw ; most specimens <130 mm. S.L. have either a mixture of uni- and tricuspids in apparently equal proportions, or one form may predominate. Fishes >135 mm. S.L. have only unicuspids in the inner series.

Osteology. The neurocranium is very similar to that of *H. serranus*. It is clearly distinct from that of *H. bayoni* (which seems to lead to the *H. mento* type) and is somewhat more substantial than the neurocranium of *H. guiarti* (which is nearest the generalized insectivore type of, say, *H. brownae*).

Vertebrae. Thirty (in the six specimens examined) comprising 13 precaudal and 17 caudal elements.

Lower pharyngeal bone triangular, the dentigerous surface noticeably broader than long. The teeth are cuspidate and slender, and are arranged in 22–24 rows ; the teeth of the two median rows are often enlarged relative to the others.

Coloration. Live fishes. In adult males the ground colour is a silvery-turquoise dorsally, shading to silver on the flanks and belly. Dorsal fin dark neutral, with black lappets and deep red maculae between the branched rays. Caudal fin dark neutral but with blood-red posterior and ventral margins. Anal dark neutral basally, black between the rays, and blood-red proximally ; the ocelli are orange-yellow and numerous. The pelvic fins are black. *Females*, have a similar ground coloration but lack the red areas on the caudal and anal fins, and the black area over the anal spines ; the pelvics are neutral and there are no anal ocelli.

Preserved material. Adult males. Ground colour brownish-grey above, becoming silver-grey on the flanks and belly. The branchiostegal membrane is sooty and there is a faint blackening on the chest and belly. Dorsal fin hyaline but with black lappets and dark maculae on the soft part. Caudal fin colourless but with numerous dark spots and streaks between the rays. Anal fin black between the spines, otherwise sooty-grey, the basal half being darker ; the greyish-white ocelli vary in number from three to seven and are arranged in one or two rows, those of the lower row being much smaller. Pelvic fins mottled black (appearing uniformly black when closed).

Females are brownish silver above and silver to silvery-yellow on the flanks and belly. All fins are colourless, the soft dorsal and the caudal sometimes weakly maculate. In some specimens there is a faint but broad and interrupted midlateral stripe from the posterior margin of the operculum to the base of the caudal fin.

Distribution. Lake Victoria.

Ecology. *Habitat*. The species has been recorded from only six different localities ; in five the bottom is of thick organic mud and in the sixth, shingle (but this place is near an area of mud) ; all localities are sheltered and the depth of water is between 20 and 40 feet.

Breeding. Very little information is available on the breeding habits of *H. victorianus*. With two exceptions (specimens 128 and 131 mm. S.L.) all the fishes examined were adult and included several individuals smaller than the exceptional juveniles. The largest fishes (166 mm. S.L.) are a male and a female.

Food. Fourteen of the twenty-seven fishes examined had ingested material in the gut. Of these, twelve had fed on fishes and two on organic mud. The fish remains are very finely divided and come from small fishes *ca*. 10–15 mm. S.L. (and this irrespective of the size of the predator). In two cases the fishes are identifiable as post-larval *Haplochromis*. The preponderance of small fishes in the prey is interesting because even in such a small sample most other predatory *Haplochromis* would have yielded remains of much larger prey fishes. There is, of course, usually some correlation between prey size and predator size, but in a sample covering a comparable size-range the prey fishes would be from 30–60 mm. S.L. Perhaps *H. victorianus* has specialized in feeding on post-larval fishes ?

The occurrence of mud in two specimens is inexplicable, particularly since there are no indications that the fishes had been feeding on insect larvae, a common alternative food in many otherwise piscivorous species.

Affinities. *Haplochromis victorianus* is very closely allied to *H. serranus* and *H. nyanzae*, see p. 161. The three species form a fairly well-defined group of deep-bodied and anatomically rather generalized species amongst the piscivorous predators of Lake Victoria.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.300 (Paratype *P. speki*) .	Entebbe .	Degen
,, 1962.3.2.478 .	Ramafuta Isl. (Buvuma channel) .	E.A.F.R.O.
,, 1962.3.2.479–82 .	Karenia, near Jinja .	,,
,, 1962.3.2.483–87 .	Pilkington Bay .	,,
,, 1962.3.2.488–494 .	Ekunu Bay .	,,
	Kenya	
Paris Museum 04 × 148 (Holotype) .	Kavirondo Bay .	,,
B.M. (N.H.).—1962.3.2.477 .	Naia Bay .	,,

Haplochromis nyanzae sp. nov.

Text-fig. 6

Pelmatochromis spekii (part) : Blgr., 1915, *Cat. Afr. Fish.*, (one specimen B.M. (N.H.) Reg. No. 1909.5.4.17).

H. serranus (part) : Regan, 1922 ; *Proc. zool. Soc. Lond.* 174 (specimen as above).

Holotype. A specimen 154·0 mm. S.L. (B.M. (N.H.) Reg. No. 1962.3.2.495) from Jinja.

Description. Based on thirteen specimens (including the holotype) 126–171 mm. S.L.

Depth of body 33·8–38·6 (M = 36·3) per cent of standard length, length of head 33·6–36·7 (M = 35·4) per cent. Dorsal head profile straight or moderately concave, sloping at an angle of 30°–40°.

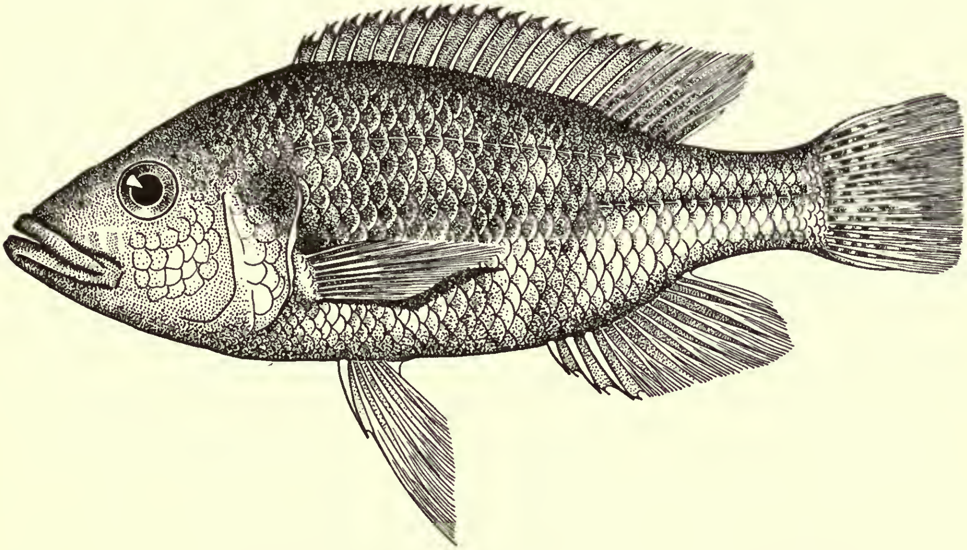

FIG. 6. *Haplochromis nyanzae* ; ·75 × N.S. (Drawn by Lavinia Beard.)

Preorbital depth 17·0–20·2 (M = 18·9) per cent of head, least interorbital width 20·0–24·5 (M = 22·2) per cent. Snout length 33·4–35·8 (M = 34·5) per cent of head, 1·0–1·1 times as long as broad. Eye diameter 19·1–24·0 (M = 22·1) per cent, ratio Eye/Preorbital 1·1–1·3 (M = 1·2), depth of cheek 24·4–27·6 (M = 25·9) per cent.

Caudal peduncle length 14·0–17·6 (M = 15·9) per cent of standard length, 1·1–1·4 (mode 1·4) times as long as deep.

Lower jaw moderately oblique, sloping at an angle of 25°–30°, anteriorly equal to the upper jaw or projecting slightly, its length 45·0–51·6 (M = 48·0) per cent of head, 1·5–2·0 (Mode 1·7) times as long as broad. The anterior outline of the dentary is smoothly curved and lacks a strong mental projection. The posterior tip of the maxilla usually reaches the vertical through the anterior orbital margin, but in some fishes it extends beyond this point or does not reach it.

Gill rakers short and stout (rarely short and slender), 8 or 9 (rarely 7 or 10) on the lower part of the first gill arch, the lowermost one or two rakers reduced.

Scales ctenoid ; lateral line with 31 (f.1), 32 (f.8) or 33 (f.4) scales, cheek with 4 or 5 (rarely 3) rows. Seven or 8 (rarely 6 or 9) scales between the dorsal fin origin and the lateral line, and between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.5) or 25 (f.8) rays, comprising 15 (f.2) or 16 (f.11) spinous and 8 (f.4), 9 (f.8) or 10 (f.1) branched rays. Anal with 12 rays (3 spinous, 9 branched) in all except one specimen which has only 2 spines and 9 rays. Pectoral fin 22·8–28·2 (M = 24·9) per cent of standard length. First pelvic ray very slightly produced in males and less so in females. Caudal truncate, scaled on its basal two-thirds.

Teeth. The *outer* row in both jaws is composed of unicuspid, moderately stout teeth, strongly incurved in most specimens, but less strongly in a few others. The number of teeth in this row shows a very slight positive correlation with standard length ; for the whole sample there are 50–76 (M = 60) upper teeth.

The *inner teeth* are uni- and tricuspid in fishes <135 mm. S.L. and unicuspid in larger fishes. There are 2–4 (usually 3) rows in the upper jaw and 2 or 3 in the lower.

Osteology. With so few specimens available, I have not been able to prepare any skeletal material. However, on comparing radiographs of this species with others of *H. victorianus* I can find no great differences in neurocranial form or general syncranial arrangement. If anything, the supraoccipital crest in *H. nyanzae* is relatively lower and the slope of the dorsal skull profile is a little less steep.

Vertebrae. 29 (f.2), 30 (f.4) or 31 (f.1), comprising 13 (f.5) or 14 (f.2) abdominal and 16 (f.3) or 17 (f.4) caudal elements.

Lower pharyngeal bone triangular, its dentigerous surface noticeably broader than long. The teeth are slender, cuspidate and arranged in 22–24 rows. Except in the most posterior transverse row or two the teeth of the median rows are not enlarged.

Coloration. Unknown in live fishes. *Preserved material. Adult males* have a dark brown ground colour with an overlying greyish tinge ; the belly, ventro-lateral aspects of the flanks, the ventral part of the preoperculum and the branchiostegal membrane are sooty. There is a distinct but narrow black lachrymal stripe, a faint black midlateral band and a fainter dorsolateral band following the upper lateral line. The lateral bands are crossed by five or six faint transverse bars. The dorsal fin is dark brown with darker spots and streaks between the soft rays. Caudal fin dark brown, anal brown with a faint and narrow darker flush along its base. Pelvic fins mottled black. In other males (whose sexual state could not be determined) the general ground coloration is much darker, the lower jaw, snout and ventral aspects of the cheek, preoperculum and operculum are black, the dorsal fin is darker (almost black) and the spots on the soft part are more obvious. The caudal fin too is darker, but the anal is similar. The anal ocelli in all males are difficult to distinguish.

Females are brown above, shading to silver-bronze on the flanks and belly. All fins are yellowish-brown, the dorsal with a grey overtone which is concentrated basally and outlined in black on the soft dorsal so that there appears to be a ventro-caudally curved dark stripe passing across it from the tip of the last spine to the middle of the last branched ray. Usually there is a dark midlateral band on the body, ending as a distinct blotch on the caudal fin base ; traces of three or four transverse bands may be visible on the flanks.

Immature and quiescent males are indistinguishable from females, although quiescent males often show a distinct darkening of the pelvic fins and faint indications of ocelli on the anal fin.

Ecology. Habitat. The available specimens of *H. nyanzae* are from five localities, of which four lie within the Napoleon Gulf and the fifth (a small island) in the nearby Buvuma Channel. In all localities the bottom is hard (shingle or rock) and the water less than twenty feet deep. The Napoleon Gulf stations are relatively sheltered but the island is exposed.

Food. Eight of the thirteen fishes examined contained food in the stomach or intestines. All eight had fed on fishes (identifiable in each case as *Haplochromis*) but one had a few insect remains in the intestine. Judging from the size of the scales and vertebrae in the gut contents, the prey fishes must have been between 30 and 60 mm. S.L.

Breeding. No data are available. All the specimens are adult.

Affinities. Haplochromis nyanzae is closely related to both *H. victorianus* and *H. serranus*. It differs from both species in the nature of the coloration in preserved males. From *H. victorianus* it is distinguished by its more oblique lower jaw (which also lacks a pronounced mental bump), shorter pectoral fin (22·8–28·2, M = 24·9% of S.L., *cf.* 26·2–32·7, M = 30·4%) and fewer teeth in the upper jaw (50–76, M = 60 ; *cf.* 64–86, M = 74). From *H. serranus* it is most readily differentiated by its rounded dentary (i.e. no pronounced mental bump), shorter lower jaw (45·0–51·6 M = 48·0, *cf.* 47·4–60·0, M = 54·3% of head) and shorter pectoral fin (22·8–28·2, M = 24·9, *cf.* 23·8–33·0 M = 27·0% of standard length).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1962.3.2.495 (Holotype)	Jinja bay	E.A.F.R.O.
,, 1962.3.2.500	Jinja pier	,,
,, 1962.3.2.501–3	Karenia (near Jinja)	,,
,, 1962.3.2.504–7	Jinja (below golf course)	,,
,, 1962.3.2.496–8	Ramafuta Isl. (Buvuma channel)	,,
,, 1909.5.4.17	Sesse Isls.	Bayon

Haplochromis bartoni sp. nov.

Text-fig. 7

Note. The trivial name is given because the species resembles *H. worthingtoni*, a species named in honour of Dr. E. Barton Worthington.

Holotype. A specimen 145·0 mm. S.L. (B.M. [N.H.] Reg. No. 1962.3.2.277) from Ekunu Bay.

Description based on thirty-five specimens (including the holotype) 135–195 mm. S.L.

Depth of body 31·4–37·9 (M = 34·0) per cent of standard length, length of head 36·2–39·7 (M = 37·5) per cent. Dorsal head profile straight or very slightly curved, sloping at about 40°; premaxillary pedicels moderately prominent, sometimes giving the profile a noticeable concavity.

Preorbital depth 17·0–22·4 (M = 20·0) per cent of head, least interorbital width 17·0–21·0 (M = 18·6) per cent. Snout 33·4–40·3 (M = 36·0) per cent of head, and 1·1–1·2 times as long as broad; diameter of eye 20·3–24·1 (M = 22·5), depth of cheek 23·4–30·2 (M = 27·0) per cent.

Caudal peduncle 13·3–17·2 (M = 15·0) per cent of standard length, 1·2–1·5 (mode 1·3) times as long as deep.

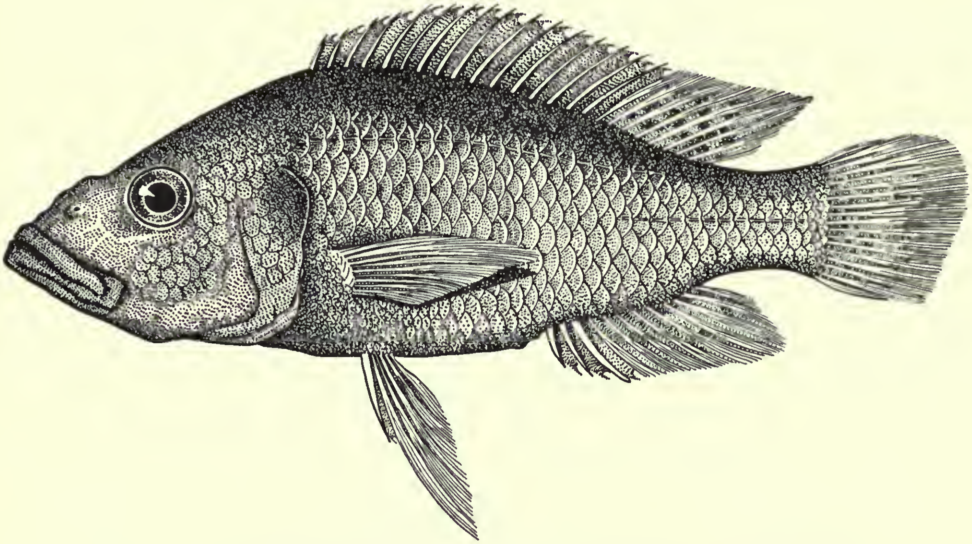

FIG. 7. *Haplochromis bartoni*; ·75 × N.S. (Drawn by Lavinia Beard.)

Mouth slightly oblique; the lower jaw sloping at *ca.* 10°–15° and projecting beyond the upper, usually with a slight mental protuberance. Length of lower jaw 50·8–57·0 (M = 52·5) per cent of head, 1·9–3·0 tines as long as broad. The medial dentigerous part of the premaxilla is not expanded anteroposteriorly. Lips slightly thickened. Posterior tip of the maxilla reaching the vertical through the anterior orbital margin in most fishes (56% of sample) and to a point slightly beyond or slightly anterior to the vertical in the remainder.

Gill rakers short and stout, 8 or 9 (rarely 7) on the lower part of the first arch, the lowermost 1–3 rakers reduced.

Scales ctenoid, lateral line with 31 (f.6), 32 (f.8), 33 (f.19) or 34 (f.2) scales, cheek with 4 (less frequently 3, rarely 5) rows. Six or 7 scales (rarely 7½) between the lateral line and the dorsal origin, 7 or 8 (rarely 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.2), 24 (f.6), 25 (f.18) or 26 (f.8) rays, comprising 14 (f.3), 15 (f.10) or 16 (f.21) spines and 8 (f.2), 9 (f.19), 10 (f.11) or 11 (f.2) branched rays. Anal fin with 11 (f.4), 12 (f.30) or 13 (f.1) rays comprising 3 spines and 8–10 branched rays. Pectoral fin 23·3–27·0 (M = 25·0) per cent of standard length. First pelvic ray slightly elongate in adult males. Caudal with a slightly oblique distal margin in many specimens, but vertically truncate in others; the obliquely truncate type is less oblique than in *H. plagiostoma* (see p. 200). The caudal is scaled on its proximal two-thirds to four-fifths.

Teeth. The *outer row* in both jaws is composed of slender, curved and unicuspid teeth, of which there are 50–80 (M = 62) in the upper jaw. The *inner rows* in most fishes >150 mm. S.L. are composed of unicuspid teeth but in most smaller fishes there is an admixture of uni- and weakly tricuspids in both jaws, or either type of tooth may predominate. In the latter case it is usually the innermost series of the upper jaw which is predominantly tri- or weakly tricuspid, the lower jaw containing mostly unicuspids. There are 2 or 3 (less frequently 4) rows in the upper jaw and 1 or 2 (very rarely 3) in the lower jaw; all inner teeth are implanted obliquely, so that in many specimens the teeth lie horizontally.

Osteology. The *neurocranium* is roughly intermediate between the *H. bayoni*-type (see p. 151) and the *H. mento*-type (see p. 176). The medial toothed part of the premaxilla is not markedly expanded, but it does show some development in that direction. This bone is, however, nearer the generalized *H. guiarti*-type than is the premaxilla of *H. bayoni.*

Vertebrae. Twenty-nine or 30 (mode), comprising 13 abdominal and 16 (f.2) or 17 (f.4) caudal elements.

Lower pharyngeal bone triangular, its dentigerous surface broader than long or equilateral; only rarely is it slightly longer than broad. The teeth are slender (but become coarser in larger fishes), cuspidate and arranged in 20–22 somewhat irregular rows.

Coloration. Live colours are unknown.

Preserved females are brown above the upper lateral line and on the dorsal surface of the head. A dark midlateral stripe runs from behind the operculum to the base of the caudal fin and, in some specimens, can also be seen on the basal half of the caudal fin membrane. Less well-defined, and absent in some fishes, is a dark band from the snout, through the eye and onto the operculum where it becomes continuous with the midlateral band. All fins colourless, the soft dorsal weakly maculate. *Adult males* are uniformly greyish-brown, except for the branchiostegal membrane, chest and belly which are sooty. Dorsal fin grey, with black lappets and dark, often coalesced maculae on the soft part. Anal fin black in the region of the spines and dark along its proximal half; distal part colourless. Anal ocelli whitish-grey, five or six in number and arranged in two rows. Caudal fin brown with dark streaks between the rays; pelvic fins black.

Distribution. Lake Victoria.

Ecology. Habitat. The species has been recorded from several different habitats, whose common features are: a depth of water less than twenty feet and the nearness of dense plant stands. The habitats include a sheltered gulf with a hard substrate, sheltered bays with deep mud bottoms, sheltered beaches with hard and soft substrates, an exposed sandy beach and a rock shelf extending from a partially exposed island. *Haplochromis bartoni* seems to be more abundant in the sheltered habitats and, from its relative scarcity in seine-net catches, it seems to be most abundant some distance offshore (between 200–300 yards).

Food. Nineteen of the thirty-one specimens examined contained food in the stomach or intestines ; all had fed exclusively on fishes and the remains could be identified as follows : Cichlidae (undetermined) (f.5), *Haplochromis* spp. (f.11), Cyprinidae (undertermined) (f.1) ; unidentifiable fish remains (f.2).

Breeding. Little information is available on this species. Sexual maturity is reached at about the same size (145 mm. S.L.) in both sexes and there is no marked dimorphism in the maximum size attained.

Affinities. Some specimens of *H. bartoni* bear a superficial resemblance to the holotype and only specimen of *H. worthingtoni*, a Lake Kyoga species. However, the likeness is purely superficial and the two species differ in several morphological characters. Within the Victoria species-flock, *H. bartoni* is somewhat isolated, not by any outstanding morphological characters but by the sum of several small characters. The neurocranium is nearest that of the *H. mento* complex but it still retains some of the more generalized characters. The premaxilla is of the specialized " beaked " type found in *H. macrognathus*. Another superficial resemblance is to the *H. serranus-H. victorianus* complex, but here the likeness is confined to general facies and is not borne out by any deeper-lying details. *Haplochromis bartoni* could represent one of the stages in the evolution of a *H. mento*-type from a *H. guiarti*-like stem, but a stage nearer the " *mento* " than the " *guiarti* " level of organization. Equally. it could link the *H. serranus* group with the *H. mento* complex, but again it would be nearer the " *mento* " than the " *serranus* " condition.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1962.3.2.277 (Holotype)	Ekunu Bay	E.A.F.R.O.
,, 1962.3.2.278–82	Ekunu Bay	,,
,, 1962.3.2.283–6	Pilkington Bay	,,
,, 1962.3.2.287–92	Ramafuta Isl. (Buvuma ch.)	,,
,, 1962.3.2.293–8	Fielding Bay	,,
,, 1962.3.2.299–300	Karenia (near Jinja)	,,
,, 1962.3.2.301	Old Bukakata	,,
,, 1962.3.2.302	Beach near Nasu point	,,
,, 1962.3.2.303–6	Jinja pier	,,
,, 1962.3.2.307–13	Jinja (below golf course)	,,

Haplochromis estor Regan 1929

Text-figs. 8 and 25

Haplochromis estor Regan, 1929, *Ann. Mag. nat. Hist.*, (10), **3**, 391.

Holotype. A specimen 153 mm. S.L. from an unknown locality in Lake Victoria, collected by M. Graham. B.M. (N.H.) Reg. No. 1959.7.2.1.

Description. Based on the holotype and eight other specimens, 141–170 mm. S.L.

Depth of body 29·6–32·4 (M = 30·3) per cent of standard length, length of head 37·2–38·5 (M = 37·8) per cent. Dorsal head profile sloping fairly steeply (*ca.* 40°), the premaxillary pedicels prominent.

Preorbital depth 19·3–20·6 (M = 19·8) per cent of head, least interorbital width 20·4–23·7 (M = 21·6) per cent. Snout 1·2–1·3 times longer than broad, its length 34·5–37·0 (M = 36·2) per cent of head; diameter of eye 20·4–23·5 (M = 21·7) per cent, depth of cheek 22·8–25·4 (M = 24·5) per cent.

Caudal peduncle 14·3–16·1 (M = 15·8) per cent of standard length, 1·3–1·6 times as long as deep.

Mouth slightly oblique (15°–20°), lower jaw always projecting, sometimes strongly so; its length 54·2–57·5 (M = 55·5) per cent of head, 2·1–2·5 times as long as broad. Lips slightly thickened, the premaxilla with the medial dentigerous surface antero-posteriorly expanded. Posterior tip of the maxilla usually reaching the vertical through the anterior orbital margin, occasionally extending somewhat behind this line.

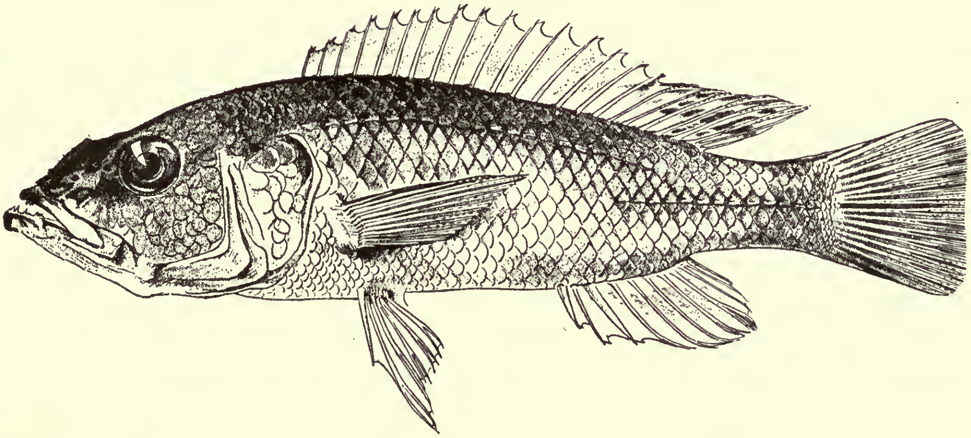

FIG. 8. *Haplochromis estor*; holotype. (Drawn by Miss M. Fasken.)

Gill rakers short and stout, 8 or 9 on the lower part of the first gill arch, the lowermost one to four rakers reduced.

Scales ctenoid, lateral line with 32 (f.3), 33 (f.5) or 34 (f.1) scales, cheek with 4 (rarely 3) series of scales; 6 or 7 (rarely $5\frac{1}{2}$ or 8) between the lateral line and the dorsal fin origin, 7 or 8 (rarely 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.1), 25 (f.5) or 26 (f.3) rays, comprising 15 (f.1) or 16 (f.8) spines and 9 (f.6) or 10 (f.3) branched rays. Anal with 11 or 12 (mode) rays, comprising 3 spines and 8 or 9 branched rays. Pectoral fin 21·8–25·3 (M = 23·6) per cent of standard length. First pelvic ray produced in males. Caudal truncate or very slightly emarginate, scaled on its basal third or half.

Teeth. The *outer row* in both jaws is composed of moderately stout, strongly curved unicuspid teeth, of which there are 52–70 (M = 60) in the upper jaw. The *inner teeth* are tricuspid in the smallest specimen examined (141 mm. S.L.) but are unicuspid in all others. These teeth are implanted obliquely and arranged in 3 or 4 (less frequently 2) rows in the upper jaw and in 2 or an irregular single row in the lower jaw.

Osteology. The neurocranium of *H. estor* is of the *H. mento* type and, because of its more ventrally curved vomer, closely approaches that of *H. dentex* (see p. 168).

Vertebrae: 29–30 comprising 12 or 13 precaudal and 16 or 17 caudal elements in the eight specimens examined.

Lower pharyngeal bone triangular, the breadth of the dentigerous surface slightly greater than its length or, less frequently, equal to its length. The teeth are relatively slender and bicuspid, and are arranged in 18–22 rows.

Coloration unknown in life. *Preserved males* (sexually active). Ground colour dark chocolate-brown above becoming dusky over silver below, especially on the chest and belly ; faint traces of a dark midlateral stripe from the opercular margin to the caudal base are sometimes visible. Lachrymal stripe broad. Lips and lower jaw almost black, the branchiostegal membrane black. Dorsal fin dark grey, the soft part maculate. Caudal fin dark grey and densely maculate, the spots on the proximal half often coalesced so that the fin is dark proximally and lighter distally. Anal greyish with an ill-defined darker band along the distal margin, and a black but narrow band along the basal part ; 2–5 grey-white ocelli are present, arranged in two rows if there are more than four ocelli. Pelvics black. *Quiescent males* have a similar coloration but are much lighter ; consequently the midlateral stripe is more obvious. The dorsal fin lacks spots.

Females are brown, shading to silver on the belly and chest ; a faint midlateral stripe, and in one specimen three very faint and incomplete vertical cross bars are visible. Dorsal fin neutral, the soft part maculate. Caudal dark and maculate. Anal and pelvic fins yellowish.

Distribution. Lake Victoria.

Ecology. Habitat. Four of the localities from which *H. estor* has been obtained are sheltered bays and gulfs where the substrate is mud and the water between 10 and 20 feet deep. No information is available for the two other localities. It can certainly be said that the species (at least when adult) does not occur commonly, if at all, in exposed inshore areas of the lake.

Food. Five of the eight specimens examined had food in the stomach and intestines. Each had fed exclusively on fishes (identifiable as *Haplochromis* in four cases and merely as " fish " in the fifth).

Breeding. No information is available. All the specimens are adult ; the two smallest are females and the rest males.

Affinities. The affinities of *H. estor* are discussed in connection with *H. dentex* (p. 169) *Haplochromis estor* is more advanced towards the extreme *H. macrognathus* type, but is nevertheless more closely allied to *H. dentex* than to *H. macrognathus* or even *H. mento.* Regan (1929) compared *H. estor* with *H. pellegrini.* There is a superficial resemblance and probably an overall phyletic relationship between the species, but it is not, in my opinion, as close as the relationships suggested above.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1962.3.2.231	Karenia (near Jinja)	E.A.F.R.O.
,, 1962.3.2.232–4	Jinja pier	,,
,, 1962.3.2.235–6	Bugungu (opp. Jinja)	,,
,, 1962.3.2.237	Entebbe	,,
,, 1962.3.2.238	Ekunu Bay	,,
,, 1962.3.2.239	Pilkington Bay	,,
	Lake Victoria, Locality Unknown	
,, 1959.7.2.1 (Holotype)		M. Graham

Haplochromis dentex Regan 1922

Text-figs. 9 and 25

Paratilapia longirostris (part) : Blgr., 1915, *Cat. Afr. Fish.*, **3**, 332.
Haplochromis dentex Regan, 1922, *Proc. zool. Soc. Lond.*, 182, pl. 3, fig. 1.

Holotype. A specimen 127·0 mm. S.L. from the Sesse Islands, B.M. (N.H.) Reg. No. 1909.5.4.1.

Description based on fifteen specimens (91·0–159·0 mm. S.L.) including the holotype.

Depth of body 24·6–29·5 (M = 26·7) per cent of standard length, length of head 33·3–36·2 (M = 34·9) per cent. Dorsal head profile gently curved, the premaxillary pedicels prominent.

Preorbital depth 18·7–24·5 (M = 21·7) per cent of head, least interorbital width 20·0–24·5 (M = 22·5) per cent. Snout longer (1·3–1·5 times) than broad, its length 36·0–41·5 (M = 38·8) per cent of head ; diameter of eye 17·3–25·7 (M = 20·4) per cent, depth of cheek 22·1–27·5 (M = 24·6) per cent.

Caudal peduncle length 17·0–19·8 (M = 18·2) per cent of standard length, 1·6–2·0 times longer than deep.

Angle of mouth variable, from almost horizontal to slightly oblique (15°–20°). Lower jaw projecting slightly, its length 43·8–49·0 (M = 46·0) per cent of head and 2·0–2·5 times its breadth. Lips moderately thickened, the medial dentigerous surface of the premaxilla expanded anteroposteriorly. Posterior tip of the maxilla not reaching the vertical through the anterior orbital margin but always behind a vertical through the posterior tip of the premaxillary pedicels.

Gill rakers moderately slender ; 9 or 10 (mode) on the lower part of the first gill arch, the lowermost one to three rakers reduced.

Scales ctenoid ; lateral line with 33 (f.10) or 34 (f.5) scales (in one specimen there are no lateral line pores on one side). Cheek with 3 or 4 (mode) rows. Five to 7 scales between the lateral line and the dorsal fin origin, 7 or 8 between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.1), 25 (f.12) or 26 (f.2) rays, comprising 15 (f.8) or 16 (f.7) spines and 9 (f.6) or 10 (f.9) branched rays. Anal fin with 11–13 rays, comprising 3 spines and 8–10 (mode 9) branched rays. Pectoral fin 20·7–25·3 (M = 24·6) per cent of standard length. Caudal truncate or weakly emarginate, scaled on its basal two-thirds. First pelvic ray produced in males.

Teeth. The *outer row* in both jaws is composed of large, well-spaced, unicuspid, moderately slender and curved teeth. There are 32–48 (M = 36) in the outer row of the upper jaw.

In all except the two smallest fishes (91 and 100 mm. S.L.) the *inner teeth* are unicuspid. The two small fishes have a mixture of unicuspids, tricuspids and weakly tricuspids, in which the unicuspids predominate. The outermost row in both jaws is composed of teeth only a little smaller than those of the outer row. There are two rows of inner teeth (sometimes irregularly arranged and giving the impression of three rows) in the upper jaw and a single (rarely) double row in the lower jaw.

Osteology. The neurocranium of *H. dentex* clearly belongs to the *H. estor-mento-macrognathus* group. The preotic part is long (65·8% of basal length), the skull is narrow and shallow (neurocranial height 3·4 times in basal length) and the supraoccipital crest is low. It differs, however, from other members of the group in its sharply decurved ethmoid-vomer region which slopes at about 40° (the neurocranial roof slopes at *ca.* 25°). In general, the neurocranium of *H. dentex* is nearest that of *H. estor*, differing mainly in having a sharply decurved vomer.

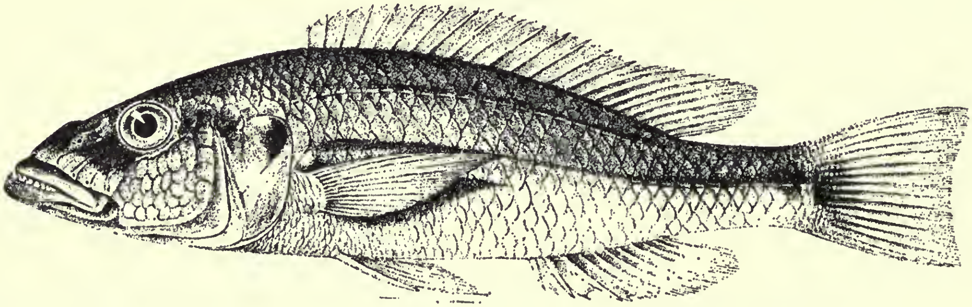

FIG. 9. *Haplochromis dentex*, holotype, ·8 × N.S. (From Regan, *Proc. zool. Soc. Lond.*)

Vertebrae. 30–32 (mode 31 in the ten specimens examined), comprising 13 (f.3) or 14 (f.7) precaudal and 16 (f.1), 17 (f.6) or 18 (f.3) caudal elements.

Lower pharyngeal bone triangular, its dentigerous surface as long as broad or slightly broader than long. The pharyngeal teeth are slender, fine and bicuspid except for the coarser and less obviously cuspidate teeth in the two median and last transverse rows. There are 18–20 rows of teeth.

Coloration. The colours of live fishes are unknown. *In preserved material* there is little difference in the coloration of males and females. The ground colour is dark grey above becoming silvery-grey below (darker in males). In some females there is a faint and narrow midlateral longitudinal stripe from the hind margin of the operculum to the caudal origin. Dorsal and caudal fins are greyish, the former with black lappets and the latter sometimes maculate. The anal and pelvic fins are hyaline in females, whereas in males the anal is greyish with a narrow black basal line running above the spines. In males there are two dead-white anal ocelli, and the pelvics are black.

Distribution. Lake Victoria.

Ecology. Habitat. Since only fifteen specimens are known, it is impossible to generalize on habitat preferences particularly since about half the specimens are from sheltered bays with mud substrates, and the others from exposed, sandy beaches, open off-shore waters with rock and shingle bottoms, and a fairly exposed gulf, also with a hard substate. The depth range extends to at least 25 feet, but the species cannot be considered common in any of the habitats investigated.

Food. Only three of the fifteen specimens available had ingested material in the gut. Two specimens had fed on small *Haplochromis* ; in the intestine of the third was a small quantity of fragmentary plant tissue.

Breeding. The breeding habits of *H. dentex* are unknown. The two smallest fishes (91 and 100 mm. S.L.) are both immature and the next largest (128 mm.) may also be a juvenile. All the other specimens (142–159 mm.) are adult.

Affinities. Superficially, *H. dentex* looks intermediate between the *H. guiarti*-type and the more specialized *H. mento-estor* types. But, closer study shows that it has greater affinity with the latter group, particularly with regard to its neurocranial form and the expanded medial dentigerous part of the premaxilla. *Haplochromis dentex* is perhaps most closely related to *H. estor*, although the latter has progressed further along the *H. mento-H. macrognathus* path of specialization. The supposed relationship between *H. dentex* and *H. estor* is based both on points of overall similarity and on likeness in the neurocrania of the two species. *Haplochromis dentex* is, however, easily distinguished by its fewer and larger teeth (mean number of teeth in the outer row of the upper jaw 37 *cf.* 60) and its shorter lower jaw (43·8–49·0, M = 46·0 per cent of head *cf.* 48·0–57·5, M = 54·9 per cent). The ancestry of *H. dentex* is obscure ; possibly it was derived from a *H. pellegrini*-like stem.

Study material and distribution records

Museum and Reg. No.		Locality		Collector
		Uganda		
B.M. (N.H.).—1909.5.4.1 (Holotype)	.	Sesse Isls.	.	Bayon
,, 1962.3.2.129	.	Sesse Isls.	.	E.A.F.R.O.
,, 1962.3.2.130–1	.	Macdonald Bay	.	,,
,, 1962.3.2.132	.	Grant Bay	.	,,
,, 1962.3.2.133–4	.	Jinja	.	,,
,, 1962.3.2.135–6	.	Buka Bay	.	,,
,, 1962.3.2.137	.	Kagera port	.	,,
,, 1962.3.2.138	.	Ramafuta Isl. (Buvuma channel)	.	,,
,, 1962.3.2.139	.	Ekunu Bay	.	,,
,, 1962.3.2.140	.	Thruston Bay	.	,,
,; 1962.3.2.142	.	Old Bukakata Bay	.	,,
		Kenya		
,, 1962.3.2.141	.	Kamiriga, Kavirondo Gulf	.	,,

Haplochromis artaxerxes sp. nov.

This peculiar species is represented by a single specimen. Its diagnostic characters are such, however, that I have little hesitation in basing the description on one fish. The specific name is derived from Artaxerxes, King of Persia, also known as *Longimanus* and alludes to the extremely long pectoral fins of this species.

Holotype a male 147·0 mm. standard length, from the Napoleon Gulf near Jinja; B.M. (N.H) Reg. No. 1962.3.2.508.

Description. Depth of body 27·9 per cent of standard length, length of head 32·7 per cent. Dorsal head profile gently curved, the premaxillary pedicels not making a prominent projection.

Preorbital depth 17·7 per cent of head, least interorbital width 20·8 per cent. Snout 1·25 times as long as broad, its length 33·3 per cent of head; eye diameter 22·9 per cent, depth of cheek 22·9 per cent.

Caudal peduncle 19·0 per cent of standard length , 1·7 times as long as deep.

Lower jaw rather flat and closing within the upper, the anterior tip projecting. Length of lower jaw 48·0 per cent of head, 2·3 times as long as broad. Median dentigerous area of the premaxilla not expanded anteroposteriorly. Posterior tip of the maxilla reaching the vertical through the anterior orbital margin. Mouth very slightly oblique, sloping at about 10°.

Gill rakers short and stout, 9 on the lower part of the first gill arch, the three lowermost rakers reduced.

Scales ctenoid; lateral line with 34 scales, cheek with 4 series. Seven scales between the lateral line and the dorsal origin, 9 between the pectoral and pelvic fin bases.

Fins. The pectoral fins of this species provide the most readily diagnostic character since they are longer (34·7% of standard length) than in any other Lake Victoria species. Only the third and fourth pectoral rays are produced so that the shape of the fin is also characteristic.

Dorsal with 15 spinous and 10 branched rays, anal with 3 spines and 9 branched rays. The distal margin of the caudal is damaged so its outline cannot be determined. The first branched pelvic ray is elongate and filamentous, in fact, intermediate between the extreme condition found in *H. bayoni* (see p. 151) and that of other species.

Teeth. Most of the outer teeth in both jaws are missing. The few remaining teeth are unicuspid, slender and very strongly curved. The inner teeth are unicuspid and arranged in two series in the upper jaw and a single, irregular row in the lower jaw.

Osteology. Neurocranial shape cannot be determined from a radiograph. There are 31 vertebrae (13 precaudal and 18 caudal). The lower pharyngeal bone is slender and triangular, the dentigerous surface being broader than long. The pharyngeal teeth are slender, fine and cuspidate, and are arranged in about twenty rows.

Coloration. Unknown in life. The *preserved adult male* is dark brown above, rapidly shading to a light brass colour with an overall greyish tinge. Lips, lower jaw, horizontal limb of the preoperculum and the posterior opercular margin black. There is a very broad (*ca.* half diameter of eye) lachrymal band and two, narrow parallel bands across the snout. Dorsal fin yellowish-brown, the soft part faintly marbled. Caudal dark, anal with a narrow, yellow basal band but otherwise sooty, particularly in the area of the spines, except for a narrow and yellow distal margin.

Ecology. The only ecological information is that the fish was caught in *ca*. 10 feet of water over a mud bottom and near a fringing stand of swamp grass. The location is near Jinja and is in the relatively sheltered Napoleon Gulf.

Diagnosis and affinities. The species is characterized by the following combination of characters: pectorals long (35% of standard length and longer than the head), the third and fourth rays greatly produced; lower jaw flat and closing within the upper jaw.

Because of these particular characters, it is difficult to suggest possible relationships for the species. The elongate pectoral is, of course, a character which could easily and suddenly develop from the pectoral of any *Haplochromis*. The lower jaw, on the other hand, requires a more fundamental change and one rarely encountered in the Victoria species flock. It is otherwise found only in some of the larval fish-eating species (Greenwood, 1959). Certainly none of these could represent the ancestral or descendant condition of a species like *H. artaxerxes*. Without any knowledge of the skeleton in this species (and especially without more information on its dentition) little can be guessed about its phyletic position. Superficially, *H. artaxerxes* does resemble *H. estor* but it is immediately distinguished by the diagnostic characters listed above, and by its shorter head and lower jaw.

Haplochromis longirostris (Hilgen.) 1888

Text-figs. 10 and 11

Paratilapia longirostris Hilgendorf, 1888, *Sitzb. ges. naturf.-Fr. Berlin*, 77; Boulenger (part), 1915, *Cat. Afr. Fish.*, **3**, 332.

Haplochromis longirostris (part); Regan, 1922, *Proc. zool. Soc. Lond.*, 187, Pl. 4, fig. 2 (two of the three specimens described *loc. cit.*).

Haplochromis gracilicauda Regan, 1922, *op. cit.*, 188, Pl. 4, fig. 2.

Haplochromis tenuis Borodin, 1931. *Proc. New Eng. zool. Club.*, **12**, 50.

The characters which Regan used to separate *H. gracilicauda* from *H. longirostris* (snout 1⅓ to 1⅔ diameter of eye *cf.* snout 1⅔ to twice diameter of eye) are really functions of growth, his species *H. gracilicauda* representing juvenile *H. longirostris*. Through the courtesy of Dr. K. Deckert of the Berlin Museum, I have been able to examine the holotype of *Paratilapia longirostris* (Z.M. Berlin Reg. No. 12744) and this confirms the identity of Regan's *H. longirostris* material. Two of these fishes (BM. [N.H.] Reg. No's. 1911.3.3.13 and 1906.5.30.516) are retained in the species but the third (B.M. [N.H.] 1906.5.30.274) is referred to *H. argenteus*.

Description based on twenty-nine specimens (including the holotype, and the syntypes of *H. gracilicauda*) 85–145 mm. S.L.

Depth of body 24·6–30·4 (M = 27·2) per cent of standard length, length of head 29·2–36·2 (M = 33·0) per cent. Dorsal head profile slightly concave or, less commonly, straight; sloping at an angle of *ca*. 30°. Premaxillary pedicels moderately prominent in large individuals.

Preorbital depth 18·2–22·5 (M = 20·8) per cent of head, least interorbital width 17·1–24·0 (M = 21·2) per cent. Snout length 32·0–38·6 (M = 36·0) per cent of head, 1·2–1·5 times as long as broad, narrowest in large fishes. Diameter of eye 18·8–24·3 (M = 21·7) per cent, depth of cheek 21·8–28·4 (M = 24·3) per cent.

Caudal peduncle 17·2–22·2 (M = 19·2) per cent of standard length, 1·7–2·3 (modal range 1·9–2·0) as long as deep.

Lower jaw markedly oblique, sloping at 40°–50°, its tip projecting slightly beyond the upper jaw in some fishes and level with it in others. Length of lower jaw 42·2–51·4 (M = 46·0) per cent of head, 2·4–3·3 times as long as broad. Lips slightly thickened, the median dentigerous part of the premaxilla not noticeably expanded. The posterior tip of the maxilla usually reaches the vertical from the posterior end of the premaxillary pedicels, or slightly beyond, but never reaches to below the anterior orbital margin.

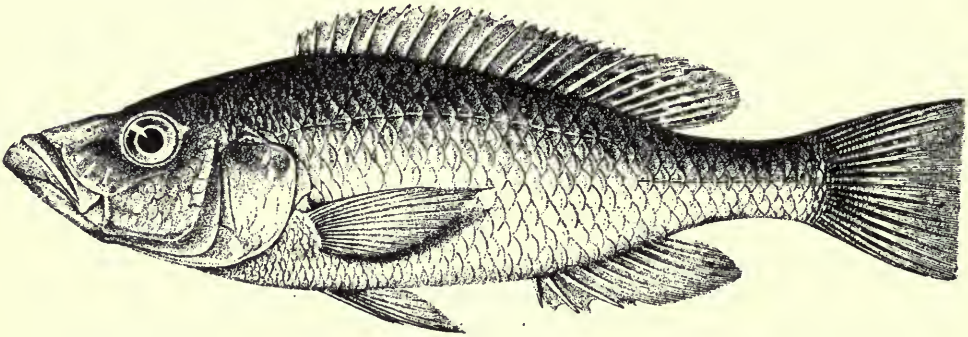

Fig. 10. *Haplochromis longirostris*, × N.S. (From Regan, *Proc. zool. Soc. Lond.*)

Gill rakers variable, from long and slender to short and stout, sometimes flattened and broadly branched ; 9–11 (rarely 8) rakers on the lower part of the first gill arch.

Scales ctenoid, lateral line with 32 (f.6), 33 (f.11) or 34 (f.12) scales, cheek with 3 or 4 rows. Five to 7 (mode 6) scales between the lateral line and the dorsal origin, 5–7 (mode 6), rarely 8, between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.4), 25 (f.19) or 26 (f.5) rays, comprising 15 (f.3), 16 (f.23) or 17 (f.2) spinous and 8 (f.4), 9 (f.18) or 10 (f.6) branched rays. The dorsal fin of the holotype is badly damaged and a count gives *ca.* 14, 9 rays. Anal fin with 11–13 rays comprising 3 spines and 8 or 9 (rarely 10) rays. Caudal truncate, scaled on its proximal two-thirds. Pectoral 20·8–25·2 (M = 23·0) per cent of standard length. First pelvic ray only slightly produced (not filamentous) in adult males.

Teeth. The *outer row* in both jaws is composed of slender and fine, moderately to strongly curved teeth, those situated posterolaterally in the upper jaw are almost hair-like. These outer teeth are unicuspid in most fishes, but in three (85·5 mm. and two of 111 mm. S.L.) there is a mixture of bi- and unicuspids or weakly bicuspids and unicuspids. There are 40–70 (M = 56) teeth in the upper jaw, the number showing no clear-cut correlation with standard length.

The *inner teeth* are either all unicuspid (fishes >125 mm S.L. and a few in the 95–

125 mm. range) or a mixture of uni- and tricuspids, unicuspids and weakly tricuspids or, as in the smallest fish (a syntype of *H. gracilicauda*), all tricuspids. The inner rows are implanted obliquely so that the teeth lie almost horizontally. There are usually 2 inner rows in the upper jaw (occasionally 3, rarely 1) and one or, less frequently, 2 in the lower jaw.

Osteology. The neurocranium barely differs from that of *H. mento* despite the more oblique angle of the lower jaw in *H. longirostris.* This greater jaw angle is apparently brought about by a slight difference in the articulatory surfaces of the quadrate and angular.

Vertebrae. 31 (f.7) or 32 (f.2) comprising 13 (f.1) or 14 (f.8) precaudal and 17 (f.6) or 18 (f.3) caudal elements.

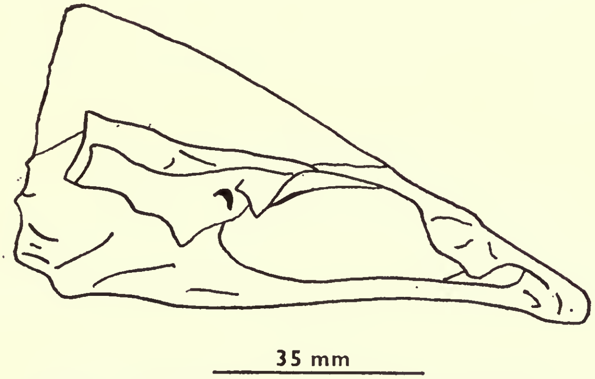

FIG. 11. *Haplochromis longirostris*, neurocranium.

Lower pharyngeal bone triangular, its dentigerous surface broader than long. The teeth are fine, cuspidate and compressed (those of the two median rows sometimes slightly enlarged) and arranged in 24–26 irregular rows.

Coloration. The colours of live fishes are unknown.

Preserved females are grey-brown above, silvery below with, on the flanks and belly, a slight brassy overtone. The lower lip and sometimes the mental area are sooty. All fins are hyaline, the dorsal with dark lappets and the caudal often densely and darkly maculate.

Sexually active males have an overall sooty appearance but with silvery areas showing through, particularly on the anterior flanks and the lateral aspects of the chest and belly ; the ventral parts of the chest and belly, however, are always darker than the dorsal parts of the body. The lower jaw, ventral part of the preoperculum and the branchiostegal membrane are intensely blank. Dorsal fin dark grey with black lappets and dark streaks between the soft rays. Caudal dark, especially on its proximal half. Anal dark, with a black area on the spinous part continued posteriorly as a narrow black band along the fin base ; the ocelli are barely visible as faint grey blotches. Pelvic fins black.

The amount of silver visible on the flanks may be correlated with the fish's state of sexual activity. *Juvenile males* are indistinguishable from females.

Distribution. Lake Victoria.

Ecology. Habitat. The species is known from only a few localities, each of which is a sandy beach either exposed to the open lake or within a sheltered gulf ; apparently *H. longirostris* is nowhere common.

Breeding. One female contains advanced embryos in the buccal cavity ; no other brooding fishes are known. Most individuals >110 mm. S.L. are sexually mature, as are some smaller fishes. Apparently both sexes reach the same maximum adult size.

Food. From the scanty data available, *H. longirostris* appears to feed on both insects (particularly pupal stages) and small fishes. Fourteen of the twenty-two specimens examined contained food. Eight had fed exclusively on insects, one on insects and fishes, and five on fishes only. The fish and insect remains were very fragmentary so identification could not be taken far. Only one fish could be identified (a small cyprinid, probably *Engraulicypris argenteus*) ; the insects are mainly pupal Bäetids.

Affinities. The slender, elongate body form and very oblique jaws of *H. longirostris* are immediate diagnostic characters and ones which isolate the species from all but one other in Lake Victoria. This other species is *H. argenteus*. *Haplochromis argenteus* differs from *H. longirostris* in having the jaws less oblique, the premaxilla more clearly " beaked " (i.e. the median toothed part expanded) and in having the eye diameter noticeably larger than the interorbital width.

On neurocranial characters, *H. longirostris* can be referred to the *H. mento* complex. But it differs from other species of this group in several character combinations and also in its mixed insect-fish diet. Phylogenetically, *H. longirostris* can be considered a somewhat isolated offshoot from the " *mento* "-group stem.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.262 (Paratype *H. gracilicauda*)	Bunjako	Degen
,, 1906.5.30.516	Bunjako	,,
,, 1906.5.30.268 (Lectotype *H. gracilicauda*)	Entebbe	,,
,, 1911.3.3.13	Jinja, Ripon Falls	Bayon
,, 1962.3.2.10–13	Jinja	E.A.F.R.O.
,, 1962.3.2.1	Grant Bay	,,
,, 1962.3.2.5	Karenia (near Jinja)	,,
,, 1962.3.2.14–25	Beach near Nasu Point	,,
	Tanganyika	
,, 1962.3.2.2	Majita Beach	,,
,, 1962.3.2.3–4	Mwanza, Capri Bay	,,
	Lake Victoria, Locality Unknown	
,, 1962.3.2.6–9		,,

Haplochromis mento Regan 1922

Text-figs. 12 and 25

Paratilapia longirostris (part) : Blgr., 1915, *Cat. Afr. Fish.*, **3**, 332, fig. 223.
Haplochromis mento Regan, 1922, *Proc. zool. Soc. Lond.*, 183.

Holotype. A specimen 174·0 mm. S.L., from Bunjako; B.M. (N.H.) Reg. No. 1906.5.30.258.

Description, based on twenty-five specimens (113–178 mm. S.L.) including the holotype.

Depth of body 24·1–31·5 (M = 28·9) per cent of standard length, length of head 31·5–37·1 (M = 34·5) per cent. There is some variation in the lateral outline of the head; in most specimens the head gives an impression of attenuation and of being pointed, but in others this impression is less marked and the head seems coarser and more bluntly rounded. There are no clear-cut morphometric differences between specimens belonging to either group, and intergrades exist.

Depth of preorbital 18·4–23·6 (M = 21·2) per cent of head, least interorbital width 20·4–24·4 (M. = 22·5) per cent. Snout 1·5–1·8 times as long as broad, its length 36·6–43·4 (M = 39·3) per cent of head; diameter of eye 16·8–22·0 (M = 19·2) per cent, depth of cheek 18·9–27·8 (M = 23·6) per cent.

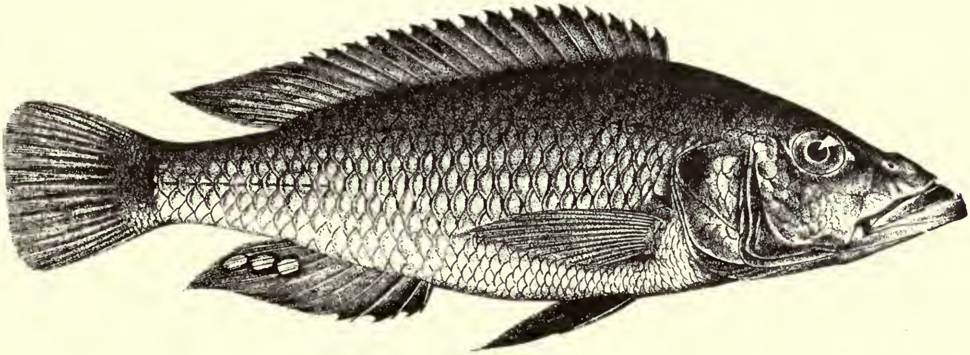

FIG. 12. *Haplochromis mento*; holotype, ·6 × N.S. (From Boulenger, *Fish. Nile.*)

Caudal peduncle length 14·1–20·9 (M = 17·5) per cent of standard length, 1·3–2·2 (modal range 1·7–1·8) times as long as deep.

Lower jaw projecting slightly in fishes <150 mm. S.L. and more markedly prominent in larger fishes; its length 41·8–50·0 (M = 46·8) per cent of head and 2·1–2·8 times as long as broad. Mouth slightly oblique or even horizontal, the medial dentigerous part of the premaxilla expanded anteroposteriorly. Posterior tip of the maxilla generally reaching to a vertical midway between the nostril and the anterior orbital margin, but sometimes extending a little more posteriorly.

Gill rakers short and stout, 8–10 (mode 9) on the lower part of the first arch, the lowermost 1–3 rakers reduced.

Scales ctenoid; lateral line with 32 (f.1), 33 (f.7), 34 (f.14) or 35 (f.3) scales, cheek with 3 or 4 (rarely 5) rows. Six or 7 (rarely 5) scales between the lateral line and the dorsal fin origin, 7 or 8 (rarely 9) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.2), 25 (f.12) or 26 (f.10) rays, comprising 13 (f.1), 15 (f.5), 16 (f.18) or 17 (f.1) spinous and 8 (f.1), 9 (f.11), 10 (f.12) or 11 (f.1) branched rays. Anal with 11, 12 (mode) or 13 rays, comprising 3 (4 in one fish) spines and 8–10 rays. Pectoral fin 19·7–24·7 (M = 23·4) per cent of standard length. First pelvic ray produced in adult males. Caudal truncate, scaled on its basal half to two-thirds.

Teeth. The *outer row* in each jaw is composed of unicuspid, very strongly curved and moderately stout teeth, there being 38–66 (M = 52) in the upper jaw. The teeth of the *inner series* are predominantly unicuspids but in a few specimens there is an admixture of unicuspid and weakly tricuspid teeth. Teeth in the outermost row of the inner series, especially in the upper jaw, are often enlarged. All inner teeth are implanted at a very oblique angle. There are 2 or 3 (rarely 4) rows in the upper jaw and 2 (rarely 1 or 3) in the lower jaw.

Osteology. The neurocranium of *H. mento* presents no outstanding specific characteristics ; it is typical of the long, shallow and narrow skull found also in *H. macrognathus*, *H. estor*, *H. gowersi* and *H. dentex*. The premaxilla shows pronounced medial expansion, a character usually associated with the " *mento* " skull type but probably more marked in this species than in the others of the group.

Lower pharyngeal bone triangular, small and fine, its dentigerous surface broader than long. The teeth are cuspidate and generally fine but some of the median series may be coarser. The teeth are rather sparsely distributed and are arranged in 16 (rarely) to 20 (most common) rows.

Vertebrae. 30–32 (mode 30) comprising 13 or 14 precaudal and 17 or 18 caudal elements (7 specimens examined).

Coloration. Live fishes. Adult males have a steely grey-blue ground colour, darker (almost sooty) on the chest and belly, branchiostegal membrane dark grey. Snout, cheek and opercular region have an irridescent sheen. The spinous part of the dorsal is irridescent blue, the soft part dark neutral ; lappets dusky. Caudal fin dark neutral. Spinous part of the anal dusky, the soft part dark neutral and bearing the dull orange-red ocelli. Pelvics black on the outer third, the remainder of the fin dusky. The colours of *live females* and *immature males* are unknown but a recently dead female has the dorsal aspects of the body and head bright green and the flanks silver. All fins are yellowish neutral.

Preserved material. Sexually active males. Ground colour brownish with a sooty overlay on the belly, the branchiostegal membrane blackish-grey and a broad but indistinct lachrymal blotch. The dorsal fin is dark brown with black lappets. Caudal dark, densely maculate on its proximal two-thirds. Anal brownish to sooty-grey, the ocelli indistinct and greyish-brown. Pelvics black on the outer third, the remaining rays black but the intervening membrane light grey. *Quiescent males* have a female-type coloration (see below) except that the pelvics are sooty on the outer three rays, the branchiostegal membrane is dark and there are faint traces of grey-white ocelli on the anal fin. The vertical bars on the flank are not always visible. *Females* are brownish-grey above, becoming golden-silver below the level of the lower lateral line. There are about nine faint vertical bars on the flank and caudal peduncle ; each bar extends from slightly above the upper lateral line to a point some one to three scales below the level of the lower lateral line. The first five bars may be joined by a midlateral stripe of about the same width as the bars. The dorsal fin is colourless or light brown, the lappets dark. The anal, caudal and pelvic fins are yellowish brown to greyish.

Distribution. Lake Victoria.

Ecology. Habitat. Haplochromis mento is apparently confined to areas where the substrate is sand or sand and rocks, and where the water is not more than twenty feet deep. Most localities from which specimens were obtained are exposed but one is a sheltered gulf; all are within two-hundred yards of the shore. the majority within one hundred yards.

Food. Eleven of the thirty-one specimens examined contained food in the stomach or intestines; of these specimens, one had only the remains of a large dragonfly larva and the others only fish remains. It is regrettable that so few specimens contained food because the prey species are predominantly cyprinid fishes; most other piscivorous *Haplochromis* seem to concentrate on cichlids. Of the ten specimens with fish in the guts, three had fed on Cichlidae (determined as *Haplochromis* in two cases) and seven on Cyprinidae (identified as *Engraulicypris argenteus* in two cases). Admittedly the contents of seven out of eleven stomachs is far too small a sample on which to base generalizations. However, it should be remembered that in samples of a like size from many other species, the identifiable food is entirely of cichlid origin and predominantly *Haplochromis*. Also, the eleven *H. mento* came from five different localities. Possibly, then, *H. mento* has specialized in preying on cyprinids, a group not heavily tapped by other piscivorous fish-predators (see Corbet, 1961).

Breeding. The species is a female mouth brooder. Fishes less than 135 mm. S.L. are immature. Possible sexual dimorphism in the maximum size attained cannot be determined from the sample available since few females are represented; the three fishes of 170 mm. S.L. and over are all males.

Affinities. Structurally, *H. mento* is a specialized predator and, therefore, shows at least group affinity with *H. estor*, *H. gowersi* and *H. longirostris*. At this level there is also some affinity between *H. mento* and *H. macrognathus*, the latter being a structurally more extreme form of *H. mento*. The affinities of these two species are discussed on p. 174. *Haplochromis estor* and *H. gowersi* both differ from *H. mento* in several ways, but primarily in the shape of the head and the more oblique jaws of the former species. Thus, it is impossible to consider *H. mento* as having any close morpho-relatives, although the species does have phyletically close affinities with several others. Since *H. mento* shows the general characters of its specialized predatory line (particularly syncranial characters) it may represent a fairly basic anatomical state in that line.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.258 (Holotype)	Bunjako	Degen
,, 1962.3.2.179–191	Beach near Nasu Point	E.A.F.R.O.
,, 1962.3.2.192	Old Bukakata Bay	,,
,, 1962.3.2.193	Between Yempita and Busiri Isls. (Buvuma Channel)	,,
,, 1962.3.2.194	Jinja (below golf course)	,,
,, 1962.3.2.195	Grant Bay	,,
,, 1962.3.2.196–7	Kagera Port	,,

Museum and Reg. No.	Locality	Collector
	Uganda (*continued*)	
B.M. (N.H.).—1962.3.2.198–200	Entebbe (airport beach)	E.A.F.R.O.
,, 1962.3.2.206–7	Entebbe Harbour	,,
,, 1962.3.2.201–5	Bukafu Bay	,,
,, 1962.3.2.209	Thruston Bay	,,
,, 1962.3.2.210–1	Ramafuta Isl. (Buvuma Channel)	,,
,, 1962.3.2.212–7	Buka Bay	,,
	Tanganyika	
,, 1962.3.2.208	Beach near Majita	,,

Haplochromis mandibularis sp. nov.

Holotype. A specimen 140·0 mm. S.L., from Jinja; B.M. (N.H.) Reg. No. 1962.3.2.222.

Description based on ten specimens (131–174 mm. S.L.) including the holotype. Only one of these specimens is a female.

Depth of body 31·6–34·3 (M = 33·1) per cent of standard length, length of head 38·0–39·3 (M = 38·6) per cent; breadth of head immeditely anterior to orbits 22·4–28·3 (M = 25·9) per cent of head length. Dorsal profile of head sloping at an angle of 30°–40°, slightly curved and becoming concave in large fishes; premaxillary pedicels slightly prominent.

Preorbital depth 17·7–20·7 (M = 19·3) per cent of head, least interorbital width 19·6–22·2 (M = 21·2) per cent. Snout 1·5–1·8 times as long as broad, its length 36·2–39·7 (M = 38·6) per cent of head; diameter of eye 17·2–22·2 (M = 19·4) per cent, depth of cheek 24·5–29·2 (M = 26·1) per cent.

Caudal peduncle 12·2–15·2 (M = 14·2) per cent of standard length, 1·0–1·3 (mode) times as long as deep.

Mouth slightly oblique, lower jaw extension variable, from projecting markedly to no extension beyond the upper jaw. Lips somewhat thickened, the median toothed portion of the premaxilla only slightly expanded anteroposteriorly. The posterior tip of the maxilla reaches a point near the anterior orbital margin in most fishes, but it extends to the level of the orbit (or even slightly beyond) in a few specimens. Lower jaw 47·3–56·8 (M = 51·5) per cent of head, 2·0–2·9 (mode 2·5) times as long as broad.

Gill rakers short and stout, 8 (mode) or 9 on the lower part of the first arch, the lowermost 1 or 2 rakers reduced.

Scales ctenoid, lateral line with 32 (f.4) or 33 (f.6) scales, cheek with 4 (rarely 5) rows. Six or 7 scales between the lateral line and the dorsal fin origin, 6 or 7 (rarely 5) between the pectoral and pelvic bases.

Fins. Dorsal with 24 (f.1), 25 (f.8) or 26 (f.1) rays, comprising 15 (f.1) or 16 (f.9) spinous and 8 (f.1), 9 (f.7) or 10 (f.2) branched rays. Anal with 12 rays, comprising 3 spines and 9 branched rays. Pectoral fin 21·4–24·3 (M = 22·2) per cent of standard length. First pelvic ray somewhat produced and filamentous in adult males. Caudal truncate, the posterior margin running somewhat obliquely forwards and downwards; scaled on the proximal half to two-thirds.

Teeth. The *outer row* in both jaws is composed of fairly stout unicuspid teeth, recurved anteriorly and strongly incurved laterally ; there are 72–94 (M = 82) teeth in the upper jaw. The *inner teeth* are all unicuspid and obliquely implanted, being arranged in 4–6 rows in the upper jaw and 2 or 3 (rarely 4) in the lower jaw.

Osteology. The neurocranium closely approaches the *H. mento-macrognathus* type but is somewhat less extreme, particularly with regard to its anterior profile which is steeper. This gives the skull a stouter and more compact appearance. The premaxilla is as beaked as that of *H. macrognathus.*

Lower pharyngeal bone triangular, its dentigerous surface as long as it is broad, but with the posterior margin deeply indented in all specimens except the two largest. The teeth are fine, cuspidate and somewhat irregularly arranged in 20–24 rows.

Coloration. The live colours are unknown. A *preserved female* is brownish-grey above, shading to silvery-brown below. On the flanks are traces of about seven dark transverse bars and there is a very weak spot on the caudal fin base. The snout and upper jaw are dark grey, the lower jaw is paler. Dorsal fin hyaline but with sooty lappets and an oblique, ventrally directed dark bar on the soft part ; the base of the soft dorsal is dark. Caudal greyish-black, the basal half densely and darkly maculate. Pelvic and anal fins hyaline, the latter with one, faint, dead-white ocellus.

Quiescent males are brownish-grey above and on the snout and upper jaw, becoming silvery below. There is an interrupted midlateral black band from the posterior opercular margin to the caudal base, where it ends as a faint spot ; the spot may extend onto the caudal fin. There are also very faint traces of an interrupted dark band running immediately above the upper lateral line. The dorsal fin is hyaline but with dusky lappets and is densely maculate on the soft part. Anal hyaline, as is the caudal although the latter is densely maculate. Pelvics faintly dusky.

Sexually active males are dark brown above, brassy on the flanks, and black ventrally, particularly on the belly, chest and branchiostegal membrane. The lower part of the preoperculum and the lower third of the operculum are also black. The dorsal fin is dusky with black lappets ; the soft part is hyaline on the distal half and densely maculate proximally. The basal third of the caudal is dark brown or black, the distal part yellowish. The anal is yellowish with a narrow black basal band and a faint black area over the last two rays ; one or two dark ocelli are present. Pelvic fins are black.

Distribution. Lake Victoria.

Ecology. Habitat. The five localities from which *H. mandibularis* were obtained are all close inshore and have a hard sand substrate ; four are in sheltered areas and one is partly exposed. The maximum depth at which the specimens could have been living is between 20 and 25 feet

Food. Five of the ten specimens examined contained food. In each case the gut contents were fishes, identifiable as *Haplochromis* in two specimens and as cichlids in the other three.

Breeding. All the specimens are adult and only one (135 mm. S.L.) is a female. No other data are available.

Affinities and diagnosis. Superficially and in many morphometric characters, *H. mandibularis* resembles *H. macrognathus.* It is distinguishable, however, by the lack of a large, well-defined black spot at the base of the caudal fin, the lack of a black mental spot and by its deeper body. An obvious difference, but one which cannot be quantified, is the shape of the head which is less compressed and less acute in *H. mandibularis* ; also in this species, at least in the size-range available, the eye diameter is equal to or is slightly larger than the preorbital depth. In *H. macrognathus* of the same size (131–174 mm.) the preorbital is deeper than the eye. Anatomically and superficially *H. mandibularis* could represent the ancestral condition from which *H. macrognathus* evolved. *Haplochromis mandibularis* also shows relationship with *H. mento* but this is less intimate than that with *H. macrognathus* ; again the relationship is of a generalized to a more specialized species.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1962.3.2.222 (Holotype)	Jinja (below golf course)	E.A.F.R.O.
,, 1962.3.2.223–4	Jinja (below golf course)	,,
,, 1962.3.2.225	Jinja Pier	,,
,, 1962.3.2.226	Bugungu (opp. Jinja)	,,
,, 1962.3.2.227–8	Beach near Nasu Point	,,
	Lake Victoria, Locality Unknown	
,, 1962.3.2.229–230		,,

Haplochromis gowersi Trewavas, 1928

Text-figs. 13 and 14

Haplochromis gowersi Trewavas, 1928, *Ann. Mag. nat. Hist.* (10), **2**, 94.

Lectotype. A specimen 154·0 mm. S.L.; B.M. (N.H.) Reg. No. 1928.5.24.478.

Description based on twenty-two specimens (145–224 mm. S.L.), including the lecto- and paratypes.

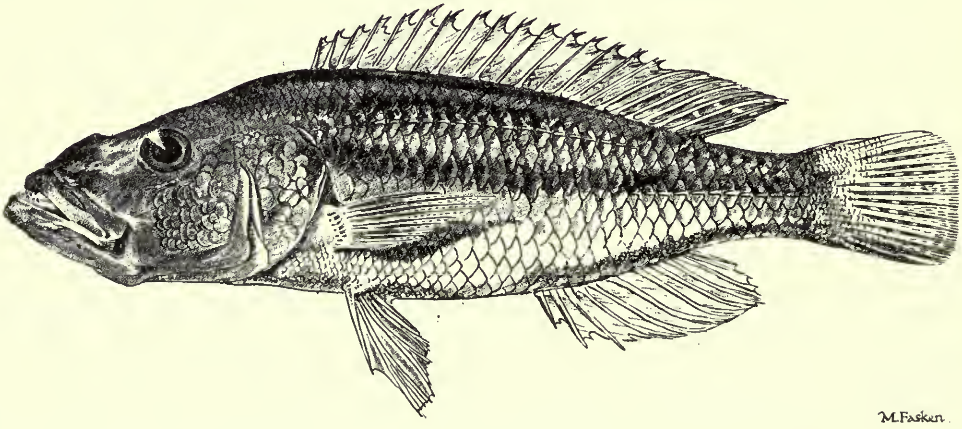

Fig. 13. *Haplochromis gowersi* ; type, ·68 × N.S. (Drawn by Miss M. Fasken.)

Depth of body 26·5–33·5 (M = 29·4) per cent of standard length, length of head 35·8–38·4 (M = 37·0) per cent. Dorsal head profile slightly curved, sloping at an angle of 30°–35°; premaxillary pedicels slightly prominent, but not sufficiently prominent to give a pronounced interorbital concavity to the profile.

Preorbital depth 19·3–24·0 (M = 22·0) per cent of head, least interorbital width 16·1–23·3 (M = 19·7) per cent. Snout 1·3–1·5 times as long as broad, its length 36·8–42·2 (M = 39·6) per cent of head; diameter of eye 15·5–19·3 (M = 17·5) per cent, depth of cheek 27·8–33·3 (M = 29·5) per cent.

Caudal peduncle 13·3–17·6 (M = 14·8) per cent of standard length, 1·3–1·6 (mode 1·4) times as long as deep.

Mouth oblique (sloping at *ca.* 30°–35°), lips slightly thickened, the median dentigerous surface of the premaxilla expanded anteroposteriorly; lower jaw always projecting but to a variable extent. Length of lower jaw 49·1–55·1 (M = 52·0) per cent of head, 2·1–2·7 times as long as broad. Posterior tip of the maxilla not reaching the vertical through the anterior orbital margin, usually reaching a point about midway between the nostril and the orbit, sometimes a little more posteriorly.

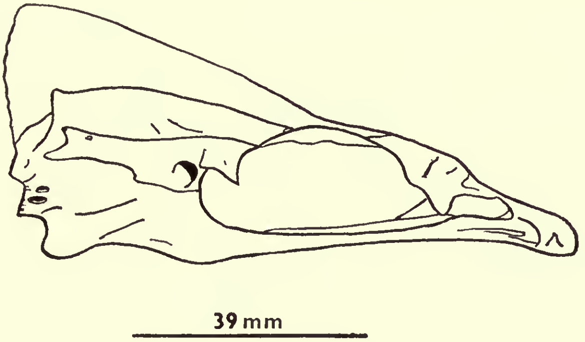

FIG. 14. *Haplochromis gowersi*, neurocranium.

Gill rakers short and stout, 8–10 (mode 9) on the lower part of the first gill arch.

Scales ctenoid; lateral line with 31 (f.3), 32 (f.2), 33 (f.8) or 34 (f.2) scales, cheek with 4 or 5 (rarely 6) rows. Six or 7 (less frequently 8) scales between the lateral line and the dorsal origin, 7 or 8 (rarely 5 or 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.1), 25 (f.10) or 26 (f.9) rays, comprising 15 (f.7) or 16 (f.13) spinous and 9 (f.7), 10 (f.11) or 11 (f.2) branched rays. Anal with 12 or 13 rays, comprising 3 spines and 9 or 10 branched rays. Pectoral fin length very variable, 17·6–27·3 (M = 20·5) per cent of standard length. First pelvic ray slightly produced in adult males. Caudal truncate, scaled on its proximal third to half.

Teeth. The *outer row* in both jaws is composed of unicuspid, moderately stout and slightly to strongly curved teeth. There are 38–52 teeth in the upper jaw, the number showing a very slight positive correlation with standard length. The *inner teeth* are unicuspid and implanted obliquely; there are 3 or 4 (mode), rarely 5 rows in the upper jaw and 2 or 3 (rarely 4 or 5) in the lower jaw.

Osteology. The *neurocranium* of *H. gowersi* is virtually identical with that of *H. mento* and is thus similar to the neurocranium of *H. estor.*

Vertebrae. Twenty-nine or 30 (mode) in the six specimens examined, comprising 13 or 14 precaudal and 16 or 17 caudal elements.

Lower pharyngeal bone triangular, the dentigerous surface longer than broad, or, less frequently, as long as broad. The teeth are moderately stout and cuspidate, and are arranged in 18–20 slightly irregular rows.

Coloration is unknown in life. *Preserved females* have a silvery ground colour, darker dorsally and on the head. A prominent and fairly broad midlateral stripe runs from the opercular margin to the caudal origin ; a fainter, narrower and sometimes partly interrupted stripe runs above the upper lateral line. In some specimens there is a faint lachrymal stripe. All fins are hyaline, the soft dorsal and the caudal are densely maculate and the former has faintly sooty lappets. *Immature males* are coloured like females except that the pelvics are darker. *Sexually active males* have a dark brown ground colour, becoming sooty from below the lateral line, with a faint golden sheen on the flanks and lower part of the operculum. Midlateral and dorsolateral stripes are developed as in females. The branchiostegal membrane is black and there is a faint, dark lachrymal stripe. The dorsal and caudal fins are dark, the anal is yellowish, sometimes with a dusky overlay which does not extend to the distal margin. There are one to three large, greyish anal ocelli. The pelvic fins are black.

Distribution. Lake Victoria.

Ecology. Habitat. The species does not appear to be confined to any particular substrate, since it is caught over both soft (mud) and hard bottoms (sand, rock, shingle) ; it is found in exposed habitats (open beaches, off-shore islands) as well as in sheltered bays and gulfs. In no locality was the water more than 20 feet deep.

Breeding. One specimen (a female 153 mm. S.L.), from a sandy beach near the Kagera river mouth, had larvae in the buccal cavity. Sexual maturity is reached at a length of about 150 mm.

Food. All the fifteen specimens with food in the stomach or intestines had fed on fishes, but in two there was also a quantity of macerated plant tissue. The fish remains were identified as : *Haplochromis* (f.9), Cichlidae (f.4) ; unidentifiable (f.2).

Affinities. As Trewavas (1928) first suggested, *H. gowersi* has affinities with *H. mento.* It differs from *H. mento* in having a deeper cheek (mean depth 29·5% of head *cf.* 23·6%), a longer lower jaw (M = 52% of head *cf.* 46·8%) and a more oblique mouth.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1928.5.24.478 (Lectotype)	Entebbe	Graham
B.M. (N.H.).—1928.5.24.479 (Paratype)	Entebbe	Graham
,, 1962.3.2.392	Williams Bay	E.A.F.R.O.
,, 1962.3.2.393–5	Beach near Nasu Point	,,
,, 1962.3.2.396–7	Karenia (near Jinja)	,,

Museum and Reg. No.	Locality	Collector
	Uganda (continued)	
B.M. (N.H.).—1962.3.2.398	Thruston Bay	E.A.F.R.O.
,, 1962.3.2.399–400	Kagera Port	,,
,, 1962.3.2.401–3	Buka Bay	,,
,, 1962.3.2.404–5	Bukassa	,,
,, 1962.3.2.406	Pilkington Bay	,,
,, 1962.3.2.407	Ramafuta Isl. (Buvuma Channel)	,,
,, 1962.3.2.409–415	Jinja Pier	,,
	Lake Victoria, Locality Unknown	
,, 1962.3.2.408		,,

Haplochromis macrognathus Regan 1922

Text-figs. 15 and 25

Paratilapia longirostris (part): Blgr., 1915, *Cat. Afr. Fish.*, **3**, 332.
Haplochromis macrognathus Regan, 1922, *Proc. zool. Soc. London*, 182; Pl. 2, fig. 2.

Holotype. A specimen 160·0 mm. S.L.; from Bunjako. B.M. (N.H.) Reg. No. 1906.5.30.260.

Description based on twenty-three specimens (including the holotype) 80–174 mm. S.L.

Depth of body 26·6–33·3 (M = 30·7) per cent of standard length, length of head 33·8–41·4 (M = 38·2) per cent. Head noticeably compressed, its breadth (as measured immediately anterior to the orbital margin) 20·4–26·0 (M = 22·9) per cent of its length. Dorsal head profile straight or slightly curved, sloping at 25°–30°; premaxillary pedicels moderately prominent and breaking the slope of the head as seen in profile.

Depth of preorbital 18·2–23·3 (M = 21·3) per cent of head, least interorbital width 16·5–22·2 (M = 18·6) per cent. Snout 1·5–2·2 times as long as broad (broadest in smaller fishes; 1·5–1·6 times), its length 33·3–44·2 (M = 39·0) per cent of head, but with indications of weak positive allometry. Diameter of eye 16·1–24·1 (M = 18·5) per cent of head, slightly greater than, or equal to the preorbital depth in fishes 80–104 mm. S.L., less than the preorbital in larger individuals. Depth of cheek 24·2–31·2 (M = 27·0) per cent.

Caudal peduncle length 13·0–20·0 (M = 15·0) per cent of standard length, 1·1–1·8 (mode 1·4) times as long as deep.

Lower jaw projecting beyond the upper, variable in extent but generally more prominent in larger fishes, its length 48·1–58·8 (M = 54·0) per cent of head and 2·7–3·5 times as long as broad. Mouth moderately oblique, the lower jaw sloping at 25°–30°; lips slightly thickened. The median dentigerous part of the premaxilla is greatly expanded anteroposteriorly so that in some specimens the premaxilla has a beak-like appearance. The posterior tip of the maxilla rarely reaches the vertical through the anterior orbital margin; usually it extends to a vertical through the posterior tip of the premaxillary pedicels.

Gill rakers short and stout, 8 (mode) or 9, rarely 10 on the lower part of the first arch, the lowermost 1–3 rakers reduced.

Scales ctenoid; lateral line with 30 (f.2), 31 (2), 32 (f.13) or 33 (f.6) scales, cheek with 3–5 (mode 4) rows. Six or 7 (rarely 8) scales between the lateral line and the dorsal origin, 6–8 between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.8), 25 (f.14) or 26 (f.1) rays, comprising 14 (f.1), 15 (f.19) or 16 (f.13) spines and 8 (f.3), 9 (f.13) or 10 (f.7) branched rays. Anal with 11 (f.3), 12 (f.18) or 13 (f.2) rays, comprising 3 spines and 8–10 branched rays. Pectoral 20·7–25·0 (M = 22·7) per cent of standard length. Pelvics with the first ray moderately produced in adult males. Caudal truncate, scaled on its proximal two-thirds, or, occasionally, as much as four-fifths.

Teeth. The *outer row* of teeth in fishes >100 mm. S.L. is composed entirely of stout, strongly curved unicuspids, but smaller fishes have an admixture of weakly bicuspid and unicuspid teeth. There are 50–100 (M = 80) teeth in the upper outer row. Teeth of the *inner series* in most fishes >110 mm. S.L. (but also in some between 95 and 100 mm.) are unicuspid; in smaller fishes there is usually a mixture of uni- and tricuspid teeth, sometimes with one type predominating in one jaw but not in the other. All the inner teeth are implanted obliquely so that in the upper jaw their crowns lie almost horizontally. The number of inner tooth rows in the upper jaw shows some positive correlation with the fish's size, there being 3–6 (mode 5) for the size range available. No such correlation exists in the lower jaw where there are 2 or 3 (less commonly 1) rows.

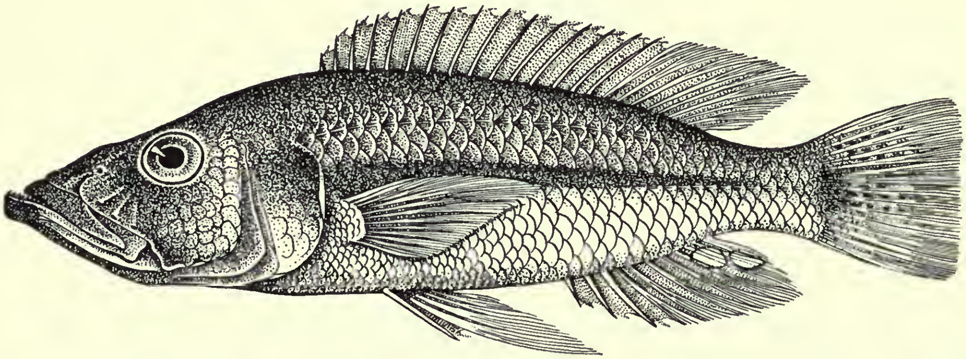

FIG. 15. *Haplochromis macrognathus*, holotype, .66 × N.S. (Drawn by Lavinia Beard.)

Osteology. The *neurocranium* is almost identical with that of *H. mento*, differing only in being slightly shallower and narrower, and in having the dorsal profile somewhat flatter. The premaxilla shows an extension of the trend seen in *H. mento* in that the median dentigerous section is greatly expanded anteroposteriorly and is almost beak-like.

Vertebrae. Twenty-nine or 30, comprising 13 or 14 precaudal and 16 or 17 caudal elements (5 specimens examined).

Lower pharyngeal bone. The outline is somewhat variable and is correlated with the head-shape of the fish. The dentigerous surface is triangular and usually equilateral but sometimes it is longer than broad, or, less frequently, broader than long.

The teeth are relatively fine (the two median rows somewhat coarser), are cuspidate and are densely crowded in 22 to 24 rows.

Coloration. The colour pattern of preserved females is a salient feature of the species, and is rare amongst Victoria *Haplochromis*. Nevertheless, it only represents the complete manifestation of the basic patterns shown in part by many species.

The colours of *live males* are unknown ; *females* are silvery-grey with a distinct midlateral black stripe on the flank and caudal peduncle, ending in a black blotch on the caudal fin near its base ; a very faint dark stripe runs slightly above the upper lateral line and there is a dark mental spot on the lower jaw. The chest is yellowish but the branchiostegal membrane is a dark saffron yellow. The dorsal fin is neutral but with dark spots and streaks between the rays. The upper half of the caudal is neutral and darkly maculate, the lower half is yellow. The anal fin is faintly yellow and the pelvics are saffron yellow.

Preserved material. Females. The ground colour is grey-brown dorsally, silver on the flanks and belly. A dark midlateral stripe runs from the eye to the caudal fin origin where it expands into a large blotch on the basal part of the fin ; the line is narrow on the head but widens shortly after it passes the posterior margin of the operculum. A second dark stripe runs slightly above the upper lateral line, from a point above the posterior opercular margin to the origin, or slightly beyond the origin of the caudal peduncle. At the base of the dorsal fin there is a series of dark spots which extend slightly upwards onto the fin membrane. There is usually a dark lachrymal spot, and always a dark blotch at the tip of the mandible. All fins, except the pelvics, are colourless although the dorsal and caudal may be darkly maculate. The pelvics are greyish, being darkest along their anterior margins.

Adult males. The ground colour is dark orange-brown. The stripes and other markings are as in females, with the addition of five or six rather faint transverse bars linking the two lateral stripes and extending a little below the lower stripe. The snout, lower jaw, branchiostegal membrane, lower limb of the preoperculum, lower part of the operculum, the chest and belly are black. The dorsal fin is sooty, the caudal dark and maculate. The anal has a black basal stripe which spreads diffusely out over most of the fin except for its distal margin which is yellowish-brown ; there are as many as six, irregularly arranged, blackish ocelli. The pelvics are black. Less sexually active males have a similar coloration but the pattern is not so intense, especially with regard to the black antero-ventral parts of the head and body.

Distribution. Lake Victoria.

Ecology. Habitat. The species has been recorded from three different habitats, viz.: sheltered gulfs with a hard substrate ; sheltered bays with a mud substrate ; and exposed, sandy beaches. From catch records it seems that *H. macrognathus* is commoner in areas where the bottom is hard than in places where it is muddy, and that the species does not occur at depths greater than twenty-five feet.

Food. Only five of the twenty specimens examined had ingested material in the stomach or intestines. Four of the five had fed exclusively on fish, and the fifth contained only fragments of plant tissue with attached colonies of blue-green algae (see also p. 144). The fish remains were identifiable in two cases as *Haplochromis*, in one as Cichlidae and in the fourth were too fragmentary for identification.

Breeding. *Haplochromis macrognathus* is a female mouth brooder. Most fishes <125 mm. S.L. are immature (one male 121 mm. S.L. was classified as " starting ") ; there is no sexual dimorphism in the maximum size attained.

Affinities. Anatomically, *Haplochromis macrognathus* belongs to the *H. mento-gowersi-estor* complex; but it is immediately distinguished from these species by the marked compression of the head and its almost beaked premaxillaries. The nearest living relative is, perhaps, *H. mandibularis* which although anatomically somewhat less specialized than *H. mento* shows certain characters (head compression, shape of mouth, coloration) strongly suggestive of the *H. macrognathus* condition.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.260 (Holotype)	Bunjako	Degen
,, 1962.3.2.420	Ekunu Bay	E.A.F.R.O.
,, 1962.3.2.421–5	Jinja Pier	,,
,, 1962.3.2.431–3	Jinja, below golf course	,,
,, 1962.3.2.434	Fielding Bay	,,
,, 1962.3.2.435	Pilkington Bay	,,
,, 1962.3.2.436	Entebbe, near Buganga	,,
,, 1962.3.2.437	Between Vempita and Busiri Isls. (Buvuma Channel)	,,
	Kenya	
,, 1962.3.2.418–9	Trawl S. of Port Southby	,,
	Tanganyika	
,, 1962.3.2.416–7	Beach near Majita	,,
,, 1962.3.2.426–430	Majita Beach	,,

Haplochromis pellegrini Regan 1922

Text-fig. 16

Paratilapia prognatha (part) : Blgr., 1915, *Cat. Afr. Fish.*, **3**, 333.
Haplochromis pellegrini Regan, 1922, *Proc. zool. Soc. Lond.*, 185, fig. 11.

Lectotype. A specimen 104·0 mm. S.L., from Entebbe, B.M. (N.H.) Reg. No. 1906.5.30.253.

Description based on twenty-five specimens (71–104 mm. S.L.) including the lecto- and paratypes.

Depth of body 29·0–33·6 (M = 31·1) per cent of standard length, length of head 34·6–37·9 (M = 36·3) per cent. Dorsal head profile sloping at *ca.* 30°, somewhat concave above the eyes, the premaxillary pedicels fairly prominent.

Depth of preorbital 15·4–22·2 (M = 17·7) per cent of head, least interorbital width 18·2–24·0 (M = 21·0) per cent. Snout longer than broad, its length 30·8–36·0 (M = 34·0) per cent of head ; diameter of eye 20·5–27·0 (M = 23·6) per cent, depth of cheek 21·4–27·0 (M = 24·3).

Caudal peduncle length 13·2–17·8 (M = 15·4) per cent of standard length, 1·1–1·5 (mode 1·3) times as long as deep.

Mouth moderately oblique; lower jaw sometimes projecting, its length 42·3–51·5 (M = 46·8) per cent of head, 1·7–2·4 (mode 2·0) times as long as broad. Posterior tip of the maxilla not reaching the vertical through the anterior orbital margin, but approaching this point in a few specimens. The median dentigerous part of the premaxilla slightly expanded anteroposteriorly.

Gill rakers moderately coarse, 7 (f.3), 8 (f.8), 9 (f.12) or 10 (f.1) on the lower part of the first arch, the lowermost 1–3 rakers reduced.

Scales ctenoid; lateral line with 30 (f.3), 31 (f.3), 32 (f.12) or 33 (f.7) scales, cheek with 3 or 4 (mode) rows; 6–8 scales between the lateral line and the dorsal fin origin, 6 or 7 (rarely 8) between the pectoral and pelvic fin bases.

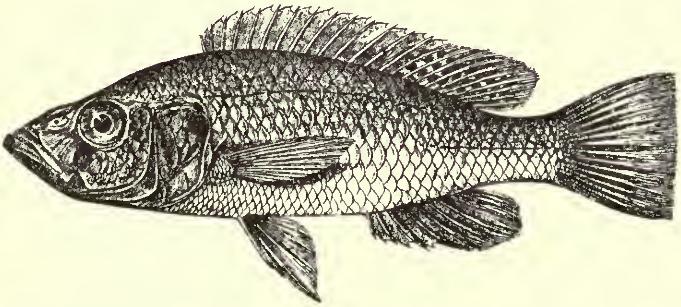

FIG. 16. *Haplochromis pellegrini*, lectotype, ·7 × N.S. (From Regan, *Proc. zool. Soc. Lond.*)

Fins. Dorsal with 23 (f.1), 24 (f.6), 25 (f.16) or 26 (f.2) rays, comprising 14 (f.5), 15 (f.13) or 16 (f.7) spinous and 9 (f.9), 10 (f.15) or 11 (f.1) branched rays. Anal with 3 spines and 8–10 (mode 9) branched rays. Pectoral fin 19·4–25·3 (M = 21·3) per cent of standard length. First ray of pelvic fin slightly produced in both sexes. Caudal truncate or subtruncate, scaled on its basal two-thirds.

Teeth. In most fishes <85 mm. S.L. the *outer row* is composed of weakly bicuspid and unicuspid teeth or only weakly bicuspids; in a few specimens this row may contain only unicuspids. Fishes >85 mm. have only unicuspid teeth in the outer row. All the outer teeth are slightly curved. The number of teeth in the upper jaw (44–62) shows slight positive correlation with standard length.

In the majority of specimens, all the *inner* teeth are tricuspid, but in some there is an admixture of tricuspids and weakly tricuspids. The inner teeth are arranged in 2 or 3 (rarely 4) rows in the upper jaw and 2 (rarely 1) in the lower.

Osteology. The neurocranium is similar to that of *H. bartoni* and *H. percoides* and does not closely approach the *H. guiarti* type. In other words it is of a type fairly advanced along the " extreme " predator line of evolution.

Lower pharyngeal bone triangular, its dentigerous surface broader than long. The teeth are fine and cuspidate, and are arranged in 22–24 rows.

Vertebrae. Twenty-eight or 29 (mode 28) comprising 13 precaudal and 15 (f.5) or 16 (f.3) caudal elements.

Coloration. Live females have a dark chocolate-brown ground colour, lighter on the chest and belly. All the fins are blackish-brown. The live colours of *males* are unknown.

Preserved material. Females. The ground colour is brownish-silver, grey on the upper surface of the head and above the upper lateral line. There is a distinct (if sometimes faint) lachrymal stripe and, in some specimens, traces of four incomplete and very faint dark vertical bars on the flanks ; the two anterior bars are crossed by a midlateral stripe originating behind the operculum but not extending beyond the first pair of bars. Dorsal fin greyish-black, as is the greater part of the caudal except for a narrow chevron of yellow-grey which extends forwards from the posterior margin. Anal greyish, pelvics yellow-brown with a sooty area at their base.

Males are uniformly dark brown, almost black, but the branchiostegal membrane is lighter ; the lachrymal stripe is very intense. The dorsal, caudal and anal fins are dark grey to sooty, the anal with two small elongate and dark ocelli. The pelvics are uniformly black except for a lighter innermost ray.

These notes are from specimens fixed in formol and preserved in alcohol. The two type specimens (both females) were fixed in alcohol and are light brown above the upper lateral line and bright silver on the flanks and belly. The dorsal fin is hyaline, with brown maculae on the basal third of the soft part. The caudal is also hyaline but is uniformly maculate. The anal and pelvic fins are colourless.

Distribution. Lake Victoria.

Ecology. Habitat. The material examined came from five localities all of which are relatively exposed sandy beaches near dense stands of submerged and emergent plants. The types came from Entebbe but no further details are known. If it is assumed that they were caught in native fishing gear (and, with regard to the date I think it reasonable to make this assumption) then the chances are greatly in favour of their having come from a similar habitat. Because of its small adult size, I cannot be certain that *H. pellegrini* does not occur in other habitats where fishing was carried out with large meshed gear (e.g. in many areas with a soft mud substrate). However, no specimens were caught in small-mesh trawls fished in these places.

Food. Of the thirty-five specimens examined, twenty-five had ingested material in the gut. In three fishes, this material was an unidentifiable sludge, in one there was sludge plus insect remains ; five had fed only on insects (principally Ephemeropteran pupae and larval Diptera) one on insects and small fishes, and fifteen had fed exclusively on fishes. The fish remains were very fragmentary but in most cases were identifiable as cichlids. The size range of the prey is 10–15 mm., that is immediately post-larval fishes. From these records it seems that *H. pellegrini* takes over from those predators which feed on embryo and larval cichlids (Greenwood, 1959). There appears to be some correlation between the diet of *H. pellegrini* and its habitat preference, since it occurs near areas where brooding cichlids congregate (e.g. reed beds).

Breeding. The species is a female mouth brooder. All the specimens seen are adults and both sexes reach the same maximum size.

Affinities. The body-form of *H. pellegrini* is similar to that of the *H. mento-H. gowersi* group and also *H. percoides*. The species is predominantly piscivorous but its small adult size is unusual for this trophic group. Anatomically it belongs to the group of moderately specialized fish-eaters, its neurocranium is fairly well advanced towards the grade of specialization shown by *H. estor* and *H. mento*, and again there is a strong resemblance to *H. percoides*. On skull and body form, *H. pellegrini* must be allocated to the group of moderately specialized predators, but there are no characters which allow one to assign it unequivocally to the *H. estor* complex or to the *H. percoides-flavipinnis* group.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.253 (Lectotype)	Entebbe	Degen
,, 1906.5.30.254 (Paratype)	Entebbe	Degen
,, 1962.3.2.510–2	Grant Bay	E.A.F.R.O.
,, 1962.3.2.513–5	Beach in Buvuma Channel	,,
,, 1962.3.2.509	Beach near Nasu Point	,,
,, 1962.3.2.516–44	Karenia (near Jinja)	,,

Haplochromis percoides Blgr. 1915

Text-figs. 17 and 25

Haplochromis percoides (part) Blgr., 1915, *Cat. Afr. Fish.*, **3**, 296, fig. 201 (the two syntypes only).
Haplochromis flavipinnis (part): Regan, 1922, *Proc. zool. Soc. Lond.*, 172 (the two syntypes of *H. percoides* only).

Lectotype. A male 79·0 mm. S.L., from Entebbe, B.M. (N.H.) Reg. No. 1906.5.30.313.

Description based on twenty specimens 67–93 mm. S.L., including the lecto- and paratype.

Depth of body 29·5–33·0 (M = 30·9) per cent of standard length, length of head 34·3–38·1 (M = 35·8) per cent. Dorsal head profile concave, the premaxillary pedicels prominent.

Preorbital depth 16·7–19·5 (M = 17·7) per cent of head, least interorbital width 19·2–22·8 (M = 20·7). Snout slightly longer than broad or as long as broad, its length 31·4–35·0 (M = 34·7) per cent of head; diameter of eye 21·9–26·6 (M = 24·2) per cent, depth of cheek 21·4–27·4 (M = 25·0).

Caudal peduncle length 12·9–16·4 (M = 15·3) per cent of standard length, 1·1–1·5 (modal range 1·4–1·5) times as long as deep.

Mouth slightly oblique, the jaws equal anteriorly or, more commonly, the lower projecting slightly. Length of lower jaw 42·3–49·2 (M = 45·2) per cent of head, 1·7–2·2 times as long as broad. Posterior tip of the maxilla close to or, occasionally, reaching the vertical through the anterior orbital margin.

Gill rakers usually slender, but in some specimens rather coarse and flat; 7–9 (mode 8) on the lower part of the first arch.

Scales ctenoid; lateral line with 30 (f.2), 31 (f.7), 32 (f.7), 33 (f.2) or 34 (f.1) scales, cheek with 3 or 4 (mode) usually imbricating but occasionally irregular rows. Six to 8 (mode 7) scales between the lateral line and the dorsal origin, 7 or 8 (rarely 6 or 9) between the pectoral and pelvic fin bases.

Fins. Dorsal with 22 (f.1), 23 (f.1), 24 (f.10), 25 (f.7) or 26 (f.1) rays, comprising 14 (f.2), 15 (f.12) or 16 (f.6) spines and 8 (f.4), 9 (f.10) or 10 (f.6) branched rays. Anal with 12 or 13 rays comprising 3 spines and 9 or 10 branched rays. Pectoral fin 22·4–26·6 (M = 24·4) per cent of standard length. First pelvic ray but slightly produced and then only in males. Caudal truncate, about the proximal half covered with small scales (*cf. H. flavipinnis*).

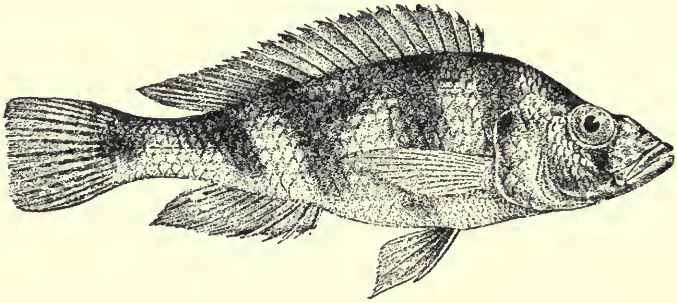

FIG. 17. *Haplochromis percoides*, lectotype ·94 × N.S. (From Boulenger, *Fish. Nile*).

Teeth in the *outer series* are predominantly unicuspid and slightly curved, but in some specimens of all sizes the lateral teeth are bi- or weakly bicuspid; there are 44–56 (mean 50) outer teeth in the upper jaw. Except in one fish (91 mm. S.L.) the *inner series* of both jaws are composed of tricuspid teeth; in the exceptional specimen all the inner teeth are unicuspid. There are 2 or 3 rows in the upper and 1 or 2 in the lower jaw.

Osteology. In its general form, the neurocranium of *H. percoides* is near that of *H. pellegrini.* The preotic face is long (67% of basal length) and its dorsal surface slopes at a gentle angle (*ca* 25°). The most noticeable difference is in the more depressed orbital region of the *H. percoides* neurocranium (reflected in the gentler slope of the dorsal surface). There is also a close resemblance between the neurocranium of *H. percoides* and that of *H. flavipinnis.* Again, the orbital region in *H. percoides* is more depressed.

The *lower pharyngeal bone* is triangular, its dentigerous surface broader than long. The teeth are slender, compressed and cuspidate, albeit weakly so in some of the anterior teeth. There are 18–22 rows of teeth.

Vertebrae. Twenty-nine, comprising 13 and 16 (f.7) or 12 and 17 (f.1) precaudal and caudal elements.

Coloration. The live colours of *H. percoides* are unknown, but judging from the well-marked vertical bands in all preserved specimens these must be conspicuous features in life. No marked sexual dimorphism is shown in the coloration of *preserved specimens,* except that the pelvic fins in males are black. The ground colour varies from silvery to dark brown ; there are five or six dark and broad transverse bands (extending from the dorsal fin base almost to the ventral midline) on the flank and caudal peduncle. Each of the two first and the two last bands are often linked by a narrow midlateral bar ; the last band frequently has a midlateral tongue extending onto the caudal fin base. Usually there are two transverse and parallel bars across the snout ; a lachrymal stripe of variable intensity is always present. The dorsal, caudal and anal fins are yellowish-orange and without other markings. The pectorals and pelvics are yellowish the latter variously dusky in males. Generally in males there is only one, ill-defined greyish blotch in the position of an anal ocellus.

Distribution. Lake Victoria.

Ecology. Habitat. The species is apparently restricted to shallow water over exposed or partly exposed sandy beaches. It is nowhere common but seems to be widely distributed around the lakeshore.

Food. Fourteen of the twenty specimens examined contained food, and all the identifiable remains were of fishes. In eight specimens the fish were small *Haplochromis* (*ca* 12 mm. S.L.), and in three the identification could not be carried beyond that of Cichlidae. In all the remaining specimens, the fish remains were too fragmentary for further identification. It was noticed that in five specimens the stomach contained four or five post-larval fishes of a similar size, thus suggesting that *H. percoides* may prey on shoals of young cichlids.

Breeding. No information is available on the breeding habits of this species. The sample studied consisted mainly of males and the only female showing signs of gonadial activity was a fish 78 mm. S.L.

Affinities. Haplochromis percoides occupies a rather isolated position amongst the Lake Victoria species, both with regard to its gross morphology and its colour pattern. The most closely related species is *H. flavipinnis.* The colour pattern of both species is virtually identical and both show a very concave upper head profile with pronounced nuchal hump. In *H. flavipinnis,* however, the jaws are inclined more steeply and the body is deeper. In details of neurocranial architecture, *H. percoides* shows a strong resemblance to *H. pellegrini* and it is conceivable that the latter species represents a stem type from which *H. percoides* evolved. There is little doubt that *H. flavipinnis* arose from an *H. percoides*-like ancestor.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.313 (Holotype)	Entebbe	Degen
,, 1962.3.2.345	Beach near Nasu Point	E.A.F.R.O.
,, 1962.3.2.346–53	Entebbe (airport beach)	,,
,, 1962.3.2.337–41	Entebbe Harbour	,,
	Tanganyika	
,, 1962.3.2.342–4	Beach near Majita	,,
,, 1962.3.2.332	Majita Beach	,,

Haplochromis flavipinnis (Blgr.) 1906

Text-figs. 18 and 19

Pelmatochromis flavipinnis Blgr., 1906, *Ann. Mag. nat. Hist.*, (7), **17**, 441 ; *Idem*, 1907, *Fish. Nile*, 448, pl. 89, fig. 3 ; *Idem*, 1915, *Cat. Afr. Fish.*, **3**, 418, fig. 286.

Haplochromis flavipinnis (part) : Regan, 1922, *Proc. zool. Soc. Londn.*, 172 (the type specimen only).

Holotype. A specimen 118·0 mm. S.L., from Bugonga ; B.M. (N.H.) Reg. No. 1906.5.30.308.

Description based on nineteen specimens (including the holotype), 69–156 mm. S.L.

Depth of body increasing allometrically with standard length, 30·8–39·2 per cent of the former. Length of head 33·6–38·0 (M = 35·8) per cent of standard length, dorsal profile concave, the concavity becoming more marked with increasing size.

Preorbital depth 16·7–21·8 (M = 19·5) per cent of head, least interorbital width 19·4–23·6 (M = 21·1) per cent. Snout as long as broad in most specimens but occasionally somewhat broader than long in fishes >130 mm. S.L. ; its length 29·2–36·4 (M = 33·3) per cent of head. Diameter of eye 19·0–25·0 (M = 21·8) per cent, depth of cheek (showing slight positive allometry) 25·0–32·7 per cent.

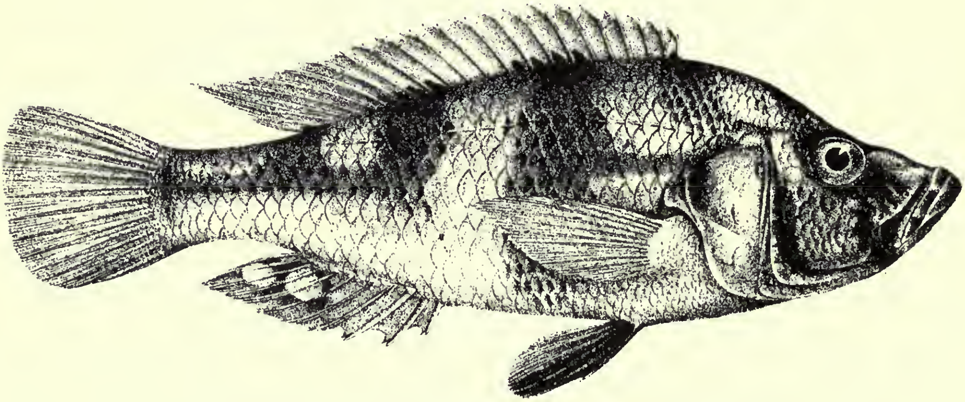

Fig. 18. *Haplochromis flavipinnis*, holotype, ·9 × N.S. (From Boulenger, *Fish. Nile.*)

Caudal peduncle length 13·8–18·6 (M = 16·0) per cent of standard length, 1·2–1·6 (modal range 1·2–1·4) times as long as deep.

Mouth oblique (sloping at 40°–50°), the lower jaw projecting slightly or, infrequently, the jaws equal anteriorly. Length of lower jaw 43·8–51·0 (M = 47·8) per cent of head, 1·6–2·0 times as long as broad. Posterior tip of the maxilla reaching or nearly reaching the vertical through the anterior orbital margin.

Gill rakers short and stout in fishes <90 mm. S.L., stout and flattened in larger individuals, 8 (mode) or 9, rarely 7 or 10, on the lower part of the first arch.

Scales ctenoid, the lateral line with 30 (f.2), 31 (f.5) 32 (f.10) or 33 (f.2) scales, cheek with 4 (mode) or 5, rarely 6 rows ; 7 or $7\frac{1}{2}$ (less frequently 8) scales between the lateral line and the dorsal origin, 7 or 8 (less frequently 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.12) or 25 (f.6) rays, comprising 15 (f.11) or 16 (f.8) spines and 8 (f.3) or 9 (f.16) branched rays. Anal with 11 (f.8) or 12 (f.11) rays, comprising 3 spines and 8 or 9 rays. Pectoral fin 23·2–29·6 (M = 25·6) per cent of standard length. Caudal fin obliquely truncate, the posterior margin sloping downwards and forwards to meet the somewhat curved ventral margin. In outline this fin resembles that of *H. plagiostoma* (see p. 200) but the lower rays do not have the appearance of regenerated structures. The caudal is truncate in the two smallest fishes examined (69 and 70 mm. S.L.) but is slightly oblique in a specimen 86 mm. S.L. At all sizes, the caudal is scaled over about two-thirds to four-fifths of its length, an unusually large area for a Lake Victoria species. The first pelvic ray is produced in adult males.

Teeth. The *outer row* of teeth in both jaws is composed of relatively slender, moderately curved unicuspids ; there are 44–66 (M = 55) teeth in the upper jaw, the number showing a very slight positive correlation with size in fishes <120 mm. S.L.

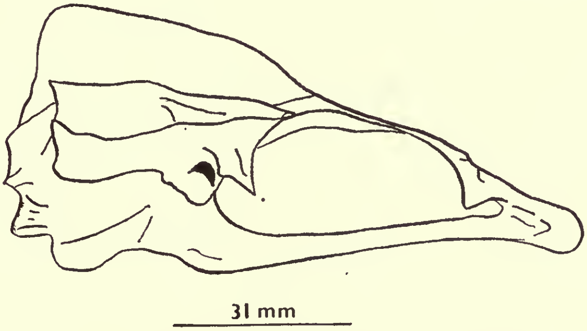

FIG. 19. *Haplochromis flavipinnis*, neurocranium.

The *inner rows* of teeth, in most individuals, are composed of unicuspids but in some fishes <100 mm. S.L. (and even in one of 150 mm.) these rows may contain a mixture of tricuspids, weakly tricuspids and unicuspids. There are 2 or 3 (less commonly 4) rows of teeth in the upper jaw and 1 or 2 rows in the lower.

Osteology. The neurocranium of *H. flavipinnis* resembles that of *H. percoides* in outline except for the shape of the supraoccipital and the points of divergence (slope of preorbital face, height in the interorbital region) are slight ; as in *H. percoides*, the neurocranium has a long preotic part (67% of basal length).

Vertebrae. Twenty-nine or 30, comprising 13 and 16 (f.6), 12 and 17 (f.2) or 14 and 16 (f.1) precaudal and caudal elements.

Lower pharyngeal bone triangular, the dentigerous surface slightly broader than long. The teeth are bicuspid and arranged in 18–20 rows, those of the two median rows are somewhat enlarged. In small fishes the teeth are relatively slender but are coarser in large individuals.

Coloration. The colours, and particularly the colour pattern, of *H. flavipinnis* are characteristic, even in preserved material.

Live colours. Adult males. Ground colour light silvery-orange dorsally, becoming greyish-black ventrally ; flanks and caudal peduncle crossed by four, broad, and dark bars. the two first becoming continuous with the dark ventral coloration. The snout and interorbital region are olivaceous, the cheek sooty ; anteriorly there is a broad-based, triangular lachrymal stripe. The dorsal fin is light olive-yellow, with dark, red-brown blotches between the soft rays. The caudal and anal fins are yellowish with an overall reddish brown tinge ; the anal ocelli are yellowish-red. Pelvic fins are black. *Adult females* have a light silver-yellow ground colour, but are dark, almost olive on the dorsal surface of the head. The body is crossed by four broad and irregular bars, the two anterior bars reaching further ventrally than the posterior pair. Dorsal fin dark neutral with darker spots on the soft part. The distal two-thirds of the caudal are dark, the proximal part is lighter. Anal fin yellow, the pelvics very light yellow except along the anterior margin where there is a brownish tinge.

Preserved material. Sexual dimorphism is less marked in fixed material, except that the chest and belly of sexually active males are dusky to black, and the entire pelvic fin is black. The ground colour is variable (probably dependent both on the fish's sexual condition if it is a male, and on preservation), from dark pinkish-brown to faintly orange-silver ; four, broad, dark and slightly irregular bars cross the flank and caudal peduncle, the two posterior bars do not extend much below the level of the lower lateral line, the two anterior bars extend (usually) almost to the ventral surface. The first and second bars are joined by a narrow midlateral stripe, as are the third and fourth bars ; from the latter there is often a posteriorly directed tongue which extends onto the base of the caudal fin. In many specimens the first three vertical bars extend upward onto the base of the dorsal fin and even part way up the fin membrane. The lachrymal stripe is a very characteristic feature, being a broad-based triangle which extends over almost half the cheek ; the remainder of the cheek is sometimes very dusky (perhaps a reflection of the fish's emotional state ?). The posterior margin of the preoperculum is outlined by a narrow vertical bar which merges dorsally with an anterior prolongation of the horizontal bar connecting the first two transverse flank bars. Often an obliquely directed, chevron-shaped interocular band is visible on the nape. The dorsal, caudal and anal fins are orange-pink or neutral, the soft dorsal maculate. In males there are three to five dead-white ocelli on the anal ; if there are more than three ocelli, they are usually arranged in two rows, the upper containing the greater number. In both sexes the pelvic spine and the first to third rays are blackish ; in sexually active males the entire fin is black.

Distribution. Lake Victoria.

Ecology. Habitat. It is impossible to generalize on the habitat preferences of *H. flavipinnis* from the data available. Specimens have been obtained from exposed sandy beaches, sheltered bays and gulfs where the substrate is of organic mud, and from rocky shelves running out from exposed islands. The only common factor in each locality has been the depth of water : less than twenty-five feet. Since *H. flavipinnis* is not abundant, nothing further could be determined.

Food. Ten of the eighteen specimens examined had food in the gut. Of these specimens, eight had fed exclusively on fishes and two contained fragments of Ephemeroptera in the stomach. The fish remains were too macerated for accurate identification beyond familial or generic levels ; in five guts the fish were identified as cichlids (and, since the scales were ctenoid, probably *Haplochromis*). No specimen had the remains of more than one fish in its stomach. The length of the prey species is estimated as ranging from 25–35 mm. S.L.

Breeding. No data are available on breeding habits. The sexes reach maturity at *ca.* 115 mm. S.L. and there is an indication that males may grow to a larger size than females.

Affinities. The coloration, and particularly the colour pattern, of *H. flavipinnis* serves as an immediate diagnostic character. It is not repeated in other Victoria *Haplochromis*. However, the transverse baring of *H. flavipinnis* is related to that of *H. percoides* (see p. 190). These two species are also related anatomically, although the jaws of *H. flavipinnis* slope more steeply and the caudal fin is obliquely truncated. Osteologically, the species show great similarity, particularly with regard to neurocranial architecture. The few differences (apart from coloration and caudal fin shape) which separate *H. flavipinnis* from *H. percoides* could be attributed to the larger adult size of *H. flavipinnis*, especially since the differences involve characters which often show differential growth rates.

Haplochromis flavipinnis also resembles *H. cavifrons*, at least anatomically, but again there are differences in coloration, in this case more marked than those between *H. percoides* and *H. flavipinnis*. The morphometric differences (e.g. the longer lower jaw and wider interorbital of *H. cavifrons*) are not correlated with size.

Phylogenetically, it seems probable that *H. flavipinnis* was derived from a small, inshore species like the present *H. percoides*, and that besides differences in coloration the evolution involved a differential growth of certain mouth-parts and associated neurocranial areas. That *H. flavipinnis* is less rigidly confined to a definite habitat may suggest that it is in the process of becoming an off-shore, mud-bottom species.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.308 (Holotype)	Bugonga	Degen
,, 1962.3.2.143–4	Ramafuta Isl. (Buvuma Channel)	E.A.F.R.O.
,, 1962.3.2.145–6	Jinja (below golf course)	,,
,, 1962.3.2.149–50	Jinja Pier	,,
,, 1962.3.2.154–5	Napoleon Gulf, near Jinja	,,
,, 1962.3.2.147	Ekunu Bay	,,
,, 1962.3.2.151–3	Entebbe Harbour	,,
,, 1962.3.2.156–8	Pilkington Bay	,,
	Tanganyika	
,, 1962.3.2.148	Majita Beach	,,
	Lake Victoria, Locality Unknown	
,, 1962.3.2.159		,,

Haplochromis cavifrons (Hilgend.) 1888

Text-figs. 20 and 21

Paratilapia cavifrons Hilgendorf, 1888, *Sitzb. Ges. nat. Fr. Berlin*, 77.
Pelmatochromis cavifrons: Blgr., 1915, *Cat. Afr. Fish.*, **3**, 419, fig. 287.
Haplochromis cavifrons: Regan, 1922, *Proc. zool. Soc. Lond.*, 183.

Description based on forty-one specimens, 108–195 mm. S.L.; I have not examined the type.

Depth of body 31·0–41·5 (M = 35·6) per cent of standard length, length of head 35·4–39·6 (M = 37·3) per cent. Dorsal head profile sloping at an angle of *ca* 30°, its outline sharply broken by the prominent premaxillary pedicels and thus appearing concave.

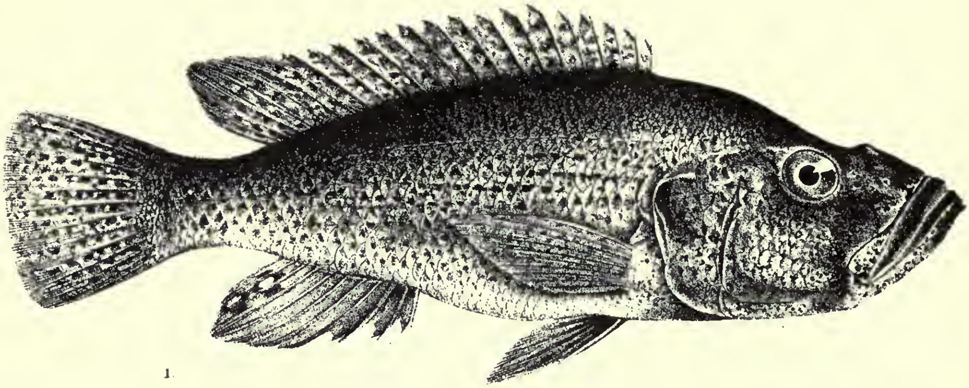

FIG. 20. *Haplochromis cavifrons*, ·75 × N.S. (From Boulenger, *Fish. Nile.*)

Preorbital depth 18·3–21·5 (M = 20·2) per cent of head, least interorbital width 21·5–27·5 (M = 25·4) per cent. Snout as long as broad, or slightly broader than long, occasionally somewhat longer than broad (the latter relationship is found most frequently in fishes <130 mm. S.L.); its length 34·0–40·0 (M = 36·5) per cent of head; diameter of eye 18·8–23·4 (M = 20·3) per cent, depth of cheek 27·2–35·4 (M = 30·2) per cent.

Caudal peduncle length 12·7–17·5 (M = 15·0) per cent of standard length, 1·0–1·4 (mode 1·3) times as long as deep.

Mouth oblique (35°–40°), the jaws equal anteriorly, or the lower projecting slightly. Lower jaw 49·3–60·5 (M = 55·5) per cent of head, its breadth contained 1·8–2·4 (mode 2·0) times in its length in fishes <175 mm. S.L., and 1·4–2·0 (mode 1·6) times in larger fishes. There is usually a broad mental projection developed at the mandibular symphysis. Posterior tip of the maxilla not reaching the vertical through the anterior orbital margin, and usually not covered by the preorbital.

Gill rakers short and stout 7 (rare)—10, mode 8, on the lower part of the first gill arch, the lowermost one or two rakers reduced.

Scales ctenoid; lateral line with 31 (f.6), 32 (f.18), 33 (f.14) or 34 (f.1) scales (in one specimen these scales are very irregularly arranged and give a count of 36); cheek with 4–6 (rarely 3) rows; 8–11 scales between the lateral line and the dorsal origin, 8 or 9 (less frequently 7 or 10) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.14) or 25 (f.25) rays, comprising 15 (f.22) or 16 (f.18) spinous and 8 (f.4), 9 (f.27) or 10 (f.9) branched rays. Anal with 11 or 12 (rarely 13) rays, comprising 3 spines and 8, 9 (mode) or 10 branched rays. Pectoral 21·7–29·3 (M = 24·7) per cent of standard length. First pelvic ray slightly produced in adult males. Caudal truncate, scaled except for the distal quarter.

Teeth. The *outer row* in both jaws is composed of unicuspid, fairly stout and slightly curved teeth. There are 56–74 (M = 63) in this row of the upper jaw.

The *inner rows* in two of the five smallest specimens (108–129 mm. S.L.) are made up of uni- and tricuspid teeth, whilst in the three others and in fishes >130 mm. S.L. the inner teeth are all unicuspids. The inner rows are implanted obliquely, and there are 2–4 (rarely 1) rows in the upper jaw and 1 or 2 (occasionally 3) in the lower.

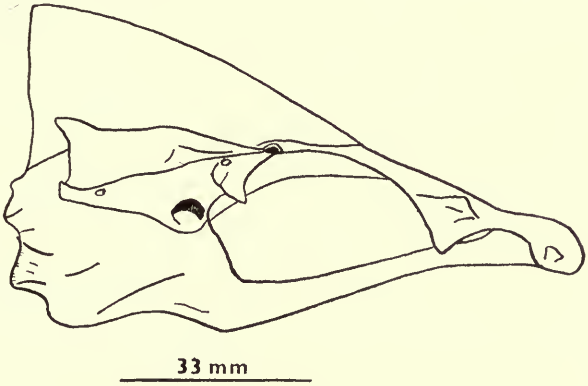

FIG. 21. *Haplochromis cavifrons*, neurocranium.

Osteology. The neurocranium is very similar to that of *H. flavipinnis*; that is, a moderately advanced type with the preorbital part sloping less steeply and the vomer not so markedly curved below the level of the parasphenoid as in the generalized forms.

Vertebrae. Twenty-nine (f.4) or 30 (f.1), comprising 13 precaudal and 16 or 17 caudal elements.

Lower pharyngeal bone triangular, the dentigerous surface as long as broad or slightly broader than long. The pharyngeal teeth are all basically bicuspid, but in larger fishes the minor cusp is vestigial except in the teeth which occupy the dorso-lateral corners of the bone. The teeth are somewhat irregularly arranged in about twenty rows.

Coloration. The densely freckled appearance of *H. cavifrons*, both alive and dead, is very characteristic. *Live colours. Adult males.* Ground colour olive to yellow-brown, shading to silvery below, the head dark brown. Both the head and body are densely speckled with brown spots and blotches. The dorsal fin is muddy yellow, sometimes (? in sexually active fishes) with traces of deep red mottling over its entire length. Caudal muddy-yellow with traces of deep red between the rays. Anal dark on its proximal third to half, muddy-red to pink distally; ocelli yellow. Pelvics are mottled black and pink, becoming blacker in sexually active males. *Females* have a similar coloration except that the pelvic and caudal fins are muddy yellow with dark blotches; the dorsal is like that of the male. Two aberrantly coloured females were caught near Mwanza (Tanganyika); in these fishes the ground colour is a dark olive green shading to light grey-green, the flecks darker green. The dorsal fin is mottled yellow-green, as is the caudal. The anal and pelvic fins are dark yellow with a faint green tinge.

Preserved material. Males. The ground colour is brown, varying from light bronze to a dark blackish-brown (in sexually active adults). The entire body and head are densely peppered with darker spots and blotches. The dorsal fin is dusky brown, marbled with darker pigment, especially on the spinous part. The caudal is brownish and faintly maculate. Anal fin light orange-brown, darker basally; ocelli faint, represented by one to three whitish spots. The pelvics are black in sexually active fishes, brownish in quiescent individuals.

Females have a similar coloration, but the ground colour is lighter and there are often traces of six, irregular and rather narrow transverse bars on the flanks and caudal peduncle. All fins, except the greyish pelvics, are as in males. One large female (190 mm. S.L.), still sexually active, has five white ocelli arranged in two rows on the anal fin.

Distribution. H. cavifrons is known definitely only from Lake Victoria; one of the specimens listed by Boulenger (1915) is from " Ripon Falls, Jinja " and may thus be from the Victoria Nile if it was caught *below* the falls.

Ecology. Habitat. It seems that *H. cavifrons* is essentially a " hard substrate " species since only two of the localities in which it was found had a mud substrate. Because the species is rare in catches from beach-operated seines, but relatively common in gill-nets set some hundred yards off-shore, it may be inferred that *H. cavifrons* is not a member of the inshore community as are, for example, *H. guiarti* and *H. bayoni*. No specimens were obtained from water more than 40 feet deep.

Food. Of the twenty-eight fishes (110–190 mm. S.L.) with ingested material in the gut, twenty-two had fed on fishes alone, two on fishes and insects and three on insects only. The insects eaten were: dragonfly larvae, chironomid larvae, and *Povilla* (Ephemeroptera) egg masses and larvae. In the individuals that had fed on fishes, the prey could be identified as follows: *Haplochromis* (f.15); Cichlidae of indeterminable genus (f.5); *Clarias* (f.1); indeterminable (f.1).

Breeding. No information was obtained on the breeding habits of *H. cavifrons*. Sexual maturity is reached in both sexes at lengths between 135 and 155 mm. S.L., and there is no dimorphism in the maximum size attained.

Affinities. No single character or combination of characters gives a clear-cut indication of the phyletic relationship of *H. cavifrons*. The coloration is unique and not easily derived from any other type now existing in the lake. Anatomically, the general suggestion is of relationships with *H. flavipinnis*, particularly with regard to head shape and mouth form. This suggestion is supported by the form of the neurocranium which is nearly identical in the two species. In turn, the same neurocranial characters associate *H. cavifrons* with *H. percoides*, a more generalized species than *H. flavipinnis*. But whereas *H. percoides* and *H. flavipinnis* have a related colour pattern, that of *H. cavifrons* is completely distinct.

It could be argued that similarity in neurocranial architecture is due to functional convergence. Against this it can be shown that similar oblique mouths and large jaws have been evolved in other species (e.g. *H. plagiostoma*) without producing a similar neurocranial shape. In fact, the neurocranium of *H. plagiostoma* is readily distinguished from that of *H. cavifrons*. If on these grounds convergence can be overruled, then *H. cavifrons* is possibly an isolated derivative from the *H. percoides* and *H. flavipinnis* stem.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.203–7	Bunjako	Degen
,, 1906.5.30.209	Buganga	,,
,, 1911.3.3.35	Jinja, Ripon Falls	Degen
,, 1962.3.2.358–65	Jinja	E.A.F.R.O.
,, 1962.3.2.354–5	Entebbe Harbour	,,
,, 1962.3.2.366–75 and 380–6	Ramafuta Isl. (Buvuma Channel)	,,
,, 1962.3.2.376–9	Pilkington Bay	,,
,, 1962.3.2.391	Bukarra (Sesse Isls.)	,,
	Kenya	
,, 1962.3.2.356	Naia Bay, Kavirondo Gulf	,,
	Tanganyika	
,, 1928.5.24.449	Mazinga Isl.	Graham
,, 1962.3.2.357	Mwanza	,,
	Lake Victoria, Locality Unknown	
,, 1962.3.2.388–90		E.A.F.R.O.

Haplochromis plagiostoma Regan 1922

Text-figs. 22 and 25

Paratilapia longirostris (part) : Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 332.
Haplochromis plagiostoma Regan, 1922, *Proc. zool. Soc. Londn.*, 181, Text-fig. 8.

Holotype : a male 113·0 mm. S.L. from Bunjako, Uganda B.M. (N.H.) reg. no. 1906.5.30.261.

Description based on thirty specimens (including the holotype) 69–147 mm. S.L.

Depth of body 32·6–39·0 (M = 36·4) per cent of standard length, length of head 34·0–37·5 (M = 36·0) per cent. Dorsal profile of head gently concave or straight, sloping at an angle of 20°–25°.

Preorbital depth 18·0–21·5 (M = 19·8) per cent of head, least interorbital width 20·6–25·0 (M = 23·4) per cent. Snout slightly broader than long or as long as it is broad, its length 28·2–35·5 (M = 32·5) per cent of the head ; depth of cheek 28·0–36·8 (M = 33·0) per cent.

Caudal peduncle 13·2–18·5 (M = 15·8) per cent of standard length and 1·0–1·5 (modal range 1·2–1·3) times as long as deep.

Mouth markedly oblique, directed upwards at an angle of 35°–50° from the horizontal : jaws equal anteriorly or, occasionally, the lower projecting slightly ; length of lower jaw 44·0–54·5 (M = 49·2) per cent of head, 1·7–2·4 (mode 2·0) times as long as broad.

Gill rakers stout but occasionally rather slender, 8 or 9 (mode), less frequently 10, on the lower part of the first arch, the lowermost 1–3 rakers reduced.

Scales ctenoid, lateral line with 30 (f.8), 31 (f.5) 32 (f.12) or 33 (f.5) scales, cheek with 4 (mode) or 5, rarely 3, rows of scales ; 5–6½ scales between the lateral line and the dorsal origin, 6 or 7 (rarely 5 or 8) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.4), 24 (f.18) or 25 (f.8) rays, comprising 14 (f.4), 15 (f.19) or 16 (f.7) spinous and 8 (f.6), 9 (f.18) or 10 (f.6) branched rays. Anal with 11, 12 or, rarely, 13 rays comprising 3 spines and 8 (mode), 9 or 10 branched rays. Pectoral fin shorter than the head, 24·6–31·0 (M = 28·1) per cent of standard length. Pelvics with the first branched ray produced, proportionately longer in adult males. The caudal fin of *H. plagiostoma* is obliquely truncate, the posterior margin sloping forward and downwards to meet the upwardly curved ventral margin. The fin shape is identical in both sexes and throughout the size range studied. The lower four or five principal rays in most specimens have the appearance of rays regenerated after damage ; commonly only one of the distal branches reaches the fin margin and sometimes neither branch extends much beyond the dichotomy. At present I cannot explain this peculiar fin shape, neither can I suggest whether it is due to some ontogenetic disturbance or to some behavioural trait of the species resulting in damage to the lower fin margin. Occasional specimens of other *Haplochromis* have an obliquely truncate caudal but *H. plagiostoma* and *H. flavipinnis* are the only species in which this peculiarity can be regarded as one of the specific characters.

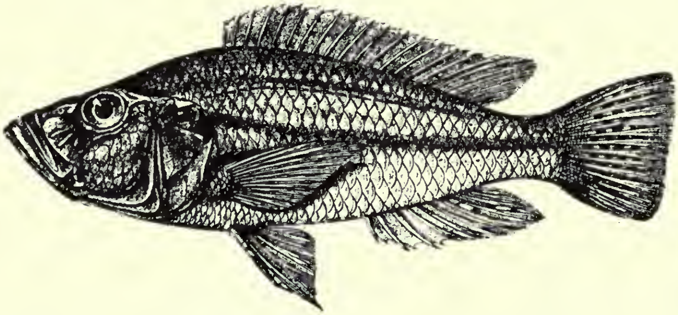

FIG. 22. *Haplochromis plagiostoma*, holotype, ·63 × N.S. (From Regan, *Proc. zool. Soc. Lond.*)

Teeth. Throughout the size range studied, the *outer row* in both jaws is composed of unicuspid, relatively stout and curved teeth, those of the upper jaw numbering 44–68 (M = 57) and somewhat more curved than the teeth of the lower jaw.

The inner rows are composed of unicuspids in all fishes >120 mm. S.L. and in some specimens in the range 70–120 mm.; other fishes in the latter size group have either all tricuspids or a mixture of uni- and tricuspid teeth. The inner teeth are arranged in 2 (less frequently 1) series in the upper jaw and 1 (less frequently 2) in the lower jaw. All these teeth are implanted obliquely, the angle sometimes approaching the horizontal.

Osteology. The neurocranium of *H. plagiostoma* is of the generalized *H. guiarti* type. Specifically, it differs from *H. guiarti* in having a slightly narrower interorbital distance and a shorter preotic region. Despite the marked difference in jaw angle of the two species (almost horizontal in *H. guiarti* and very oblique in *H. plagiostoma*) the interspecific differences in syncranial proportions and morphology are slight. The steep jaw angle is brought about by several minor changes. For example, the gentler slope of the ethmoid region (over which the premaxillary pedicels slide) allows the dentigerous area of the premaxilla to lie at a greater angle from the horizontal, thus matching the increased slope of the dentary. The latter gains its slope from slight changes in the articular surfaces of the quadrate and angular which allow the dentary to move dorsally through a wider arc than is the case in *H. guiarti.* There is also a compensatory change in neurocranial proportions. The preotic part of the skull in *H. plagiostoma* is relatively shorter than in *H. guiarti.* This shortening of the anterior part of the skull, correlated with a relatively longer dentary and more mobile hinge, allows the dorsal (i.e. most anterior part of the gape) to be moved from a position near the horizontal to one nearer the vertical. The lengthening of the lower jaw permits this change without causing any alteration in the near vertical angle of the hyomandibula.

The *lower pharyngeal bone* is triangular, its dentigerous area as long as broad or slightly longer than broad. The teeth are coarse and cuspidate, those of the two median rows being slightly enlarged ; there are 16–20 rows of teeth.

Vertebrae. Twenty-eight (f.1) or 29 (f.9), comprising 12 (f.2) or 13 (f.8) precaudal and 15 (f.1), 16 (f.7) or 17 (f.2) caudal elements.

Coloration in life. Sexually active males are light blue-grey on the flanks and postero-ventral surfaces, smokey grey dorsally and on the chest (which is darker than the back). The head is smokey-grey with lighter blue flecks on the cheek and operculum ; the branchiostegal membrane is sooty with a blue overlay. The dorsal fin is dark grey with deep crimson spots between the posterior spines and over the entire soft part ; the lappets and the margin of the soft dorsal are deep crimson. The caudal is dark with a crimson margin and spots on the proximal half. The anal is deep red, the ocelli (one to four arranged in a single row) yolk-yellow. The pelvics are black. In *quiescent males* the ground colour is more silvery, the dorsal fin less intensely coloured and the anal is hyaline except for a red flush which is most intense along the margin of the fin.

Females are silver with a faint powder-blue sheen posteriorly on the flanks and faint midlateral and dorsolateral stripes, the latter much shorter than the former.

Colour in preserved material. Females are brownish above, silvery below. There is a broad midlateral band, sometimes of irregular thickness, running from behind the operculum to the caudal origin ; a distinct but often faint lachrymal stripe is generally present. All the fins are hyaline but the caudal is densely maculate. *Sexually active males* are brownish above shading to a greyish copper on the flanks, and becoming sooty on the chest and belly ; the branchiostegal membrane is black. There is often a midlateral stripe but rarely are there any transverse bars ; a lachrymal stripe is usually visible. The dorsal, caudal and anal fins are brownish and sometimes faintly dusky. In some specimens there is a narrow black band on the dorsal fin, running obliquely backwards and downwards from the lappet of the last spine to about the middle of the last branched ray. The pelvics are black. The anal ocelli (1–4, usually 2) are opaque and are arranged in a single row.

Distribution. Lake Victoria.

Ecology. Habitat. The species has been caught over both soft (organic mud) and hard (sand and shingle) substrates. Common features of all localities are their sheltered nature (gulfs and bays) and relatively shallow depths (never more than 30 feet).

Food. Although *H. plagiostoma* is one of the commoner species, little is known about its feeding habits. The reason for this is the high frequency of fishes without food in the gut on capture. Those specimens with food (twenty-two in all) are exclusively piscivorous, the prey species being predominantly *Haplochromis* and, less often, small Cyprinidae (probably *Engraulicypris argenteus*). The two smallest fishes examined (81 and 91 mm. S.L.) had fed on fishes; the stomach of the smaller individual contained two post-larval *Haplochromis* (S.L., *ca.* 8 mm.).

Breeding. A single female (107 mm. S.L.) has been recorded with eggs in the mouth; this specimen is also the smallest sexually mature individual in the collection. One larger fish (115 mm. S.L.) is immature, but all other specimens 112 mm. S.L. and above are adult. Females may reach a larger size than males but I have insufficient material to confirm this point.

Affinities. No close relative of *H. plagiostoma* has been found amongst the present-day *Haplochromis* of Lake Victoria. The species is immediately characterized by its oblique mouth, obliquely truncated caudal fin and lack of distinct transverse bars on the body. Only one other species, *H. flavipinnis*, has an obliquely truncated caudal developed in all individuals, but its coloration is an obvious diagnostic character. An oblique mouth is not uncommon amongst the piscivorous species, but is usually associated with a different type of skull architecture than that of *H. plagiostoma*, which retains the basic *H. guiarti*-type. The nature of the neurocranium, the body-form and the male coloration all suggest that *H. plagiostoma* should be placed with the *H. victorianus-H. serranus* species-group, but representing an anatomically rather specialized offshoot. The other members of this group have typical subtruncate caudal fins and horizontal or slightly oblique mouths.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1906.5.30.261 (Holotype)	Bunjako	Degen
,, 1962.3.2.438–9	Sesse Isls.	E.A.F.R.O.
,, 1962.3.2.440	Jinja (below golf course)	,,
,, 1962.3.2.446	Jinja, Pier	,,
,, 1962.3.2.441	Karenia (near Jinja)	,,
,, 1962.3.2.442	Buvuma Isl.	,,
,, 1962.3.2.443–5	Thruston Bay	,,
,, 1962.3.2.448–64	Pilkington Bay	,,
,, 1962.3.2.465–73	Ekunu Bay	,,
,, 1962.3.2.474–6	Buka Bay	,,
	Lake Victoria, Locality Unknown	
,, 1962.3.2.447		,,

Haplochromis michaeli Trewavas 1928

Text-figs. 23 and 24

Haplochromis michaeli Trewavas, 1928, *Ann. Mag. nat. Hist.*, (10), **2**, 93.

Note. I have already drawn attention (Greenwood, 1960) to a mistake over the identity of the two syntypes of *H. michaeli*. The two specimens which were thought to be the syntypes are actually referrable to a species now named *H. empodisma*. Before this error was realised, these specimens were used as the basis for comparison with other species. Thus, references to *H. michaeli* made in any of my papers published before 1960 should be corrected to read *H. empodisma*. I have no doubt about the identity of the specimens now considered to be the types of *H. michaeli*.

Lectotype. A specimen 145·0 mm. S.L., from Rusinga Island ; B.M. (N.H.) Reg. No. 1928.5.24.487.

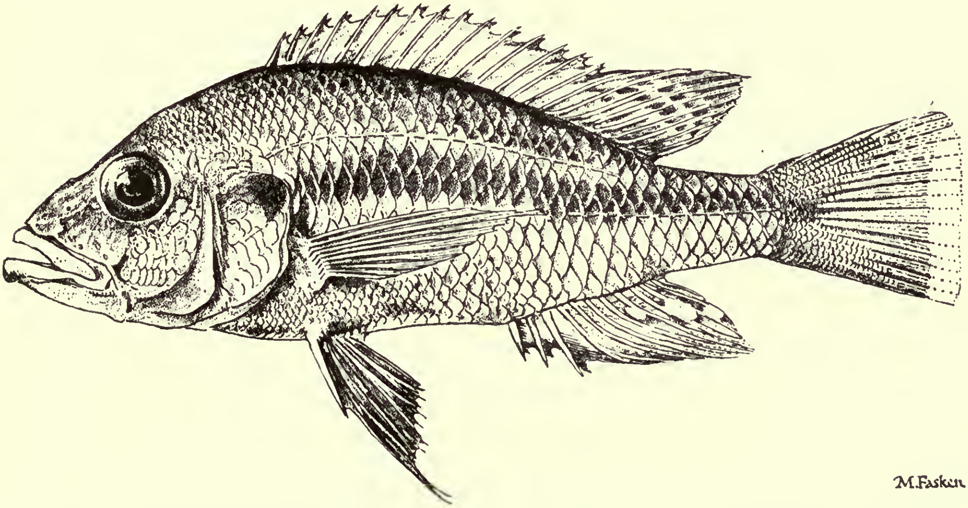

FIG. 23. *Haplochromis michaeli*, lectotype, ·7 × N.S. (Drawn by Miss M. Fasken.)

Description based on twenty-one specimens, 117–145 mm. S.L. (including the lecto- and paratype).

Depth of body 30·8–37·6 (M = 34·3) per cent of standard length, length of head 33·8–38·4 (M = 36·2) per cent. Dorsal head profile straight or slightly curved, if straight often with a gentle interorbital concavity.

Preorbital depth 14·8–19·2 (M = 17·4) per cent of head ; least interorbital width 24·8–29·4 (M = 26·6) per cent. Snout length 32·6–38·0 (M = 34·7) per cent of head, 1·0–1·2 times as long as broad ; diameter of eye 24·0–29·1 (M = 27·0), depth of cheek 22·9–27·7 (M = 25·8) per cent of head.

Caudal peduncle length 15·8–19·7 (M = 17·3) per cent of standard length, 1·3–1·9 (modal range 1·5–1·6) as long as deep.

Lower jaw slightly oblique, projecting a little in some specimens and always with a pronounced mental bump at the symphysis ; its length 43·3–53·5 (M = 48·0) per cent of head, 1·6–2·4 times as long as broad (modal range 1·8–2·0). Lips somewhat thickened, the posterior tip of the maxilla extending to below the pupil in most fishes but only to below the anterior part of the eye in others.

Gill rakers variable, from short but slender to short and stout ; 8–10 (mode 9) rakers on the lower part of the first gill arch.

Scales ctenoid ; lateral line with 31 (f.1), 32 (f.7), 33 (f.8), 34 (f.3) or 35 (f.2) scales, cheek with 3 or 4 rows. Six or 7 scales between the lateral line and the origin of the dorsal fin, 7 or 8 (rarely 6 or 9) between the pectoral and pelvic fin bases. The scales of the chest are noticeably small.

Fins. Dorsal with 24 (f.10), 25 (f.10) or 26 (f.1) rays, comprising 15 (f.19) or 16 (f.2) spinous and 9 (f.12), 10 (f.8) or 11 (f.1) branched rays. Anal with 11 (f.12), 12 (f.7) or 13 (f.1) rays, comprising 3 spines and 8 (f.12), 9 (f.7) or 10 (f.1) branched elements. In one specimen, only two spines are present in the anal. The caudal is truncate and scaled on its basal half to two-thirds. The first pelvic ray is slightly produced and filamentous in adult males. Pectoral fin 24·1–30·4 (M = 26·2) per cent of standard length.

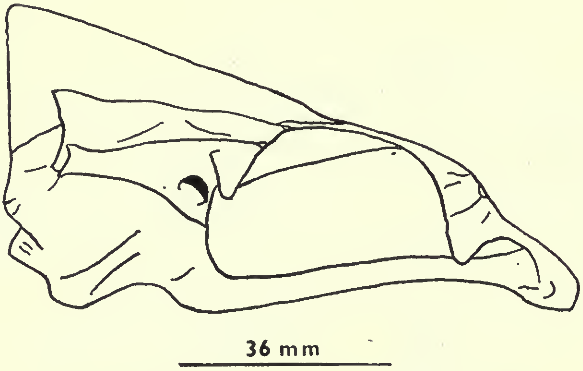

FIG. 24. *Haplochromis michaeli*, neurocranium.

Teeth. The *outer row* in each jaw is composed of slender, slightly curved and unicuspid teeth, of which there are 60–82 (M = 66) in the upper jaw.

The *inner teeth* are either all unicuspids or a mixture of uni- and weakly tricuspids ; there is apparently no correlation between the nature of the inner teeth and the size of the fish. In one exceptional specimen some of the inner teeth are bicuspid and the remainder are tricuspid. There are 3 (rarely 2 or 4) inner rows in the upper jaw and 2 or 3 (rarely 1) in the lower jaw.

Osteology. The *neurocranium* is of the generalized predator type and compares closely with *H. guiarti* or *H. serranus*. It differs from the generalized non-predator type (e.g. *H. brownae*) only in the somewhat more elongate preotic part of the skull (65% of basal length, *cf.* 55%) and consequently in the less steeply sloping dorsal profile. There is also an associated lengthening of the dentary as compared with *H. brownae*.

Vertebrae. Thirty (in all seven specimens examined), comprising 13 precaudal and 17 caudal elements.

Lower pharyngeal bone triangular, the dentigerous surface slightly to noticeably broader than long. The teeth are small, slender and cuspidate, occasionally with the two median rows composed of stouter teeth. The dental arrangement is irregular ; the teeth are spaced and arranged in 22–24 rows.

Coloration. The colours of live fishes are unknown : *Preserved females* are brown above and yellowish below the well-defined, broad midlateral dark stripe. This stripe is often broken into two parts of variable length ; it ends posteriorly at the base of the caudal fin. In some fishes there are traces of four, short and faint transverse bars on the flank ; a dark lachrymal blotch is often present. All the fins are grey or greyish-yellow, the soft dorsal and the caudal are maculate.

Adult males are brown above the midlateral stripe and on the head ; the stripe and occasional transverse bars are as in females, but the lachrymal marking is often in the form of a full stripe from the orbit to the angle of the jaws. Below the midlateral stripe, the colour is brassy-silver or greyish silver with the chest and ventral abdominal surfaces dusky, as is the branchiostegal membrane. All fins (except the pelvics) are sooty-brown, the dorsal with black lappets and darkened membrane between the branched rays. The caudal is maculate, the anal has a black patch across the spinous part and a black band along the distal margin of the fin. The anal ocelli (when present) are small and ill-defined black areas, four to five in number and arranged in a single line. The pelvics are black.

Distribution. Lake Victoria.

Ecology. Habitat. The species has been collected in only five different localities but in each the habitat was similar : a mud substrate in a sheltered gulf or bay, or, in the lee of a large island. The depth of water varied from 10–50 feet ; all the specimens were caught in nets set on the bottom and within two-hundred yards of the shore. The exact locality at which the type specimens were collected is not known, nor have I been able to check the identity of specimens listed as *H. michaeli* in Graham's (1929) catch records ; apparently these specimens are no longer in the Museum.

Food. Seven of the fourteen specimens examined contained food in the gut. Six of these had fed exclusively on fishes (unidentifiable) ; the other specimen had ingested large quantities of plant material, none of which showed signs of digestion.

Breeding. No data are available on the breeding habits of this species. The smallest fish (117 mm. S.L.) is immature and the next larger (127 mm.) is adult. The largest male is 138 mm. S.L. and the three largest specimens (141–145 mm.) are females.

Affinities. The nearest relative of *H. michaeli*, at least on anatomical grounds, is *H. martini* (see Greenwood, 1960). The external characters (excluding coloration) which separate the species are : the smaller eye of *H. michaeli* (24·0–29·1 (M = 27·0) of head *cf.* 29·4–37·5 (M = 31·7) per cent), its longer lower jaw (43·3–53·5 (M = 48·0) per cent of head, *cf.* 38·4–45·8 (M = 42·6) per cent), the predominance of unicuspid teeth in the outer row of both jaws (this row in larger *H. martini* [90–100 mm. S.L.] contains both bi- and unicuspids) and a less strongly decurved dorsal head profile. The yellow coloration of live and immediately *postmortem H. martini* is outstanding, and the *post mortem* colours of *H. michaeli* do not suggest any similarity. The preserved colour patterns of the two species are basically similar yet in *H. martini* an upper, interrupted lateral band is always present and the midlateral stripe rarely extends onto the caudal fin base as is usual in *H. michaeli*.

The morphological and anatomical differences between the species are slight and could well be the result of differential growth, particularly since the smallest specimen of *H. michaeli* is 13 mm. longer than the largest *H. martini*. As *H. martini* are sexually mature at a standard length of 80 mm. but *H. michaeli* are still immature at 117 mm. S.L., there can be little reason to suppose that " *H. michaeli* " specimens are merely large individuals of *H. martini*. But I do suggest that the species are very closely related and that *H. michaeli* evolved from an *H. martini*-like stem, one of its divergent characters (and biologically the most important) being the greater size attained. Like *H. martini*, *Haplochromis michaeli* represents a slight deviation from the generalized insectivore type and does not show any great anatomical specialization adapting it for its role as a piscivorous predator. The most obvious specialization *vis a vis* the generalized insectivore, is the larger gape and longer lower jaw, a character also developed in *H. martini*.

The resemblance between *H. michaeli* and *H. empodisma* is entirely superficial. The species belong to different phyletic lines, *H. michaeli* to one with only two extant species and *H. empodisma* to a longer line which includes the extant assemblage of mollusc-eating species (*H. pharyngomylus*, *H. ishmaeli* and *H. obtusidens* ; see Greenwood, 1960).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1962.3.2.314	Sesse Isls.	E.A.F.R.O.
,, 1962.3.2.315	Buvuma Isl.	,,
,, 1962.3.2.316–7	Fielding Bay	,,
,, 1962.3.2.318	Bugungu Bay (opp. Jinja)	,,
,, 1962.3.2.319	Ekunu Bay	,,
,, 1962.3.2.320–31	Pilkington Bay	,,
	Kenya	
,, 1928.5.24.487 (Lectotype)	Rusinga Isl.	Graham
,, 1928.5.24.488 (Paratype)	Rusinga Isl.	Graham

DISCUSSION

Evolution and Phylogeny

The piscivorous species form a large element of the Lake Victoria species-flock. I estimate that about 40 per cent of the known species are predominantly fish-eating. The specialized predators on embryo and larval fishes (Greenwood, 1959) are included in this estimate.

Like the majority of *Haplochromis* in the Lake, the predators probably evolved from one or two insectivorous species. There is no direct evidence to suggest that they evolved from an originally fluviatile piscivorous stem species. The present-day fluviatile predators are clearly more differentiated from the generalized *Haplochromis* than are the predatory *Haplochromis* of Lake Victoria. In fact, the most widely distributed species are placed in the genus *Serranochromis* which, despite its obviously close relationship to *Haplochromis*, is distinguishable from any predatory *Haplochromis* of Lake Victoria.

Within the Victoria species-flock there is one species, *H. brownae*, which seems to provide annectant feeding habits and certain anatomical details linking the generalized insectivores with the anatomically least specialized piscivores.

The anatomical characters involved in the evolution of the predator group are relatively simple and may be summarized as follows :

(i) An increase in adult size relative to species in other trophic groups ; the modal adult size-range for the species described here is 140–160 mm. S.L., whereas for the majority of non-piscivores it is 80–100 mm. Amongst the fish-eating predators there are exceptions to this generalization ; for example *H. percoides* and *H. pellegrini* with a modal adult length of 100 mm. Species showing the most specialized anatomical traits invariably belong to groups having the largest adult size-ranges.

(ii) A differential lengthening in the neurocranium. It appears that only the preotic region of the skull is involved in this relative growth. The changed proportions of the preotic skull are shown in the following figures. In adult non-piscivores of a generalized type (or even those with specialized feeding habits like algal-grazing) the preotic portion comprises some 55–58% of the neurocranial length. The proportion is probably affected by the adult size of the fish since in certain of the larger species (e.g. *H. ishmaeli*, a mollusc-crusher, or *H. empodisma* an insectivore) the preotic length is from 57 to 62% of neurocranial length. Intraspecifically it appears that there are insignificant ontogenetic changes in preotic proportion, at least over the latter part of the growth range. (e.g. in *Haplochromis mento* the preotic proportion in neurocrania of 25 and 30 mm. length is 66 and 67% respectively).

Amongst the piscivores the preotic proportion is from 62·0–71·0 (mean *ca.* 66·0) per cent, the figures being based on one adult neurocranium for each of the species described above except *H. artaxerxes*. Again, the differences in proportion cannot be entirely due to differences in neurocranial size. For example, the preotic is 71% in a 31 mm. neurocranium of *H. flavipinnis* but only 66% in a 38 mm. skull of *H. dentex*.

There are correlated changes in several syncranial characters. Two obvious changes are the relative lengthening of the lower jaw and deepening of the cheek region. The latter represents a general lengthening of the suspensorium and a broadening of the pterygoid bones ; it is used as a measure of these changes because it is easily determined by direct mensuration.

The lower jaw does not always lengthen in proportion to the lengthening of the preotic region, and the jaw may be relatively longer in one of two species with equal preotic proportions. In such a case, the lower jaw either projects beyond the upper or the suspensorium is greatly lengthened and the angle of the closed mouth becomes very oblique. The latter condition is seen in *H. plagiostoma* where the preotic proportion is 62% of the neurocranium, the lower jaw is 49% of the head length and the

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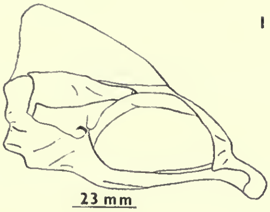

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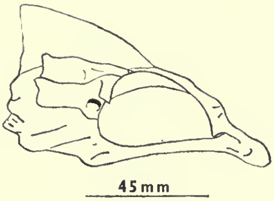

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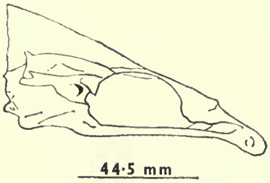

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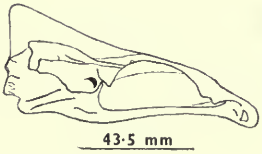

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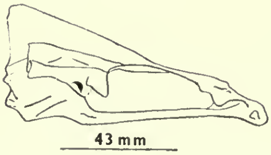

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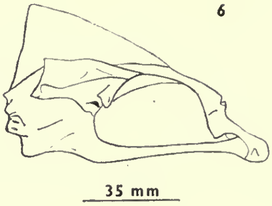

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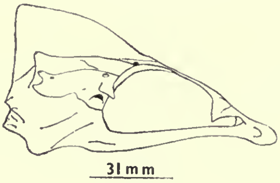

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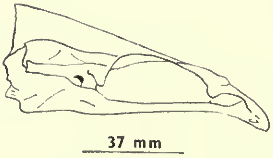

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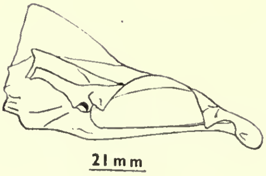

cheek is 33% of the head. These figures may be compared with *H. guiarti* (a species with a near horizontal mouth) where the preotic length is 65·5% of the neurocranium, the lower jaw 44·4% of the head length and the cheek only 25%.

(iii) Other changes in neurocranial proportions are a narrowing of the entire neurocranium and a decrease in its height, particularly of the otic-occipital region and the supraoccipital crest. Correlated with the decrease in height is a decrease in slope of the dorsal surface of the skull. This particular group of characters is not, however, a general one and many predatory species retain a skull whose outline (except for the longer preotic region) differs little from the generalized *Haplochromis* type. The slope of the dorsal surface, especially in the ethmoid region, affects the angle at which the premaxilla lies and hence the angle of the jaws. Species with a gently sloping ethmoid region tend to have the mouth more oblique than those with a steep ethmoid angle. Broadly associated with neurocranial outline is the body shape of the fish. Species with elongate, shallow neurocrania tend to have a slender elongate body shape, whilst the deeper bodied species have taller neurocrania.

(iv) A general character amongst the piscivores is the presence of unicuspid, curved and often strong teeth in the outer row of both jaws. However, in those species showing the greatest anatomical specialization, all or most of the teeth in small (i.e. juvenile) specimens are of the generalized bicuspid type. The pharyngeal teeth are generally few in number, moderately stout and with simple bicuspid or weakly bicuspid crowns. The oro-pharyngeal dentition as a whole is one adapted for gripping and macerating, not, as in many non-cichlid predators, merely for gripping the prey before it is bolted whole.

These, then, are the principal character complexes involved in the anatomical evolution of predatory species from a presumed insectivore stem.

In other morphological characters, such as the number of vertebrae, scales and fin rays, the piscivores do not differ from the generalized species. In this respect the Lake Victoria *Haplochromis* differ from those of Lake Nyasa. There, many species with a predatory facies and with piscivorous habits have more vertebrae and fin rays than do the generalized species. (I am indebted to Dr. E. Trewavas for giving me data on certain Nyasa species and for discussing this point with me).

Fig. 25. Diagram illustrating (in the left-hand column) the main evolutionary trend in neurocranial shape amongst the predatory species, from the generalized predator (1 and 2) to the "extreme" form (4 and 5). In the right-hand column, each neurocranium (except that of *H. guiarti*, No. 6) is a representative of the principal species or species group deviating from the major trend in other syncranial characters. *Haplochromis guiarti* represents a slight modification of the condition found in *H. brownae* (see text, p. 207).

All neurocrania are drawn to the same basal length ; the actual length is shown below each specimen.

(1) *H. brownae*	(2) *H. serranus*	(3) *H. mento*
(4) *H. estor*	(5) *H. macrognathus*	(6) *H. guiarti*
(7) *H. plagiostoma*	(8) *H. dentex*	(9) *H. percoides*

Because this paper only deals with a representative sample of the Lake Victoria predators, it is not possible to discuss fully the phyletic relationship of the various species. When I have finished working on the other predatory species some clearer picture may emerge. At present a few supposedly phyletic groups can be recognized. Many species, although showing the broad characterization of either the " generalized predator " type (exemplified by *H. serranus*) or the " extreme predator " type (as seen in *H. macrognathus*), do not exhibit particularly close relationship with other living species. It is certainly more difficult to separate the predators into groups than it is to divide the non-predators into possible phyletic assemblages. One reason for this is, of course, the fact that the non-predators are divisible into phyletic-trophic groups on the basis of anatomical adaptations to a particular feeding habit. Convergence and parallelism do occur but are usually recognizable as affecting whole subgroups and not merely a single species. Amongst the predators the problem is complicated by the relatively few characters with which to build a group facies.

Despite such difficulties it does seem possible to reconstruct a putative ancestral type from which the base of the predator stem could have emerged. *Haplochromis brownae* may show the early stages of evolution leading from an insectivore towards a fully piscivorous predator. Anatomically, there are indications of some prospective adaptations for evolution in that direction. The mixed insect and small-fish diet is another important link. In most respects, however, *H. brownae* is very close to the extant and widespread, usually fluviatile species which we think must resemble the early colonizers of Lake Victoria.

From an *H. brownae*-like stem it is easy to imagine how the *H. serranus*, *H. victorianus*, *H. nyanzae* group was evolved. The species show some new characters (longer preotic skull, unicuspid teeth in the jaws) which may be the result of the larger adult size attained, but which may have evolved independently. Related to the *H. serranus* group is *H. plagiostoma*, an isolated species with very oblique jaws but a neurocranium of the type found in *H. serranus* and its allies.

Another " generalized " predator, but at a slightly higher level of differentiation, is *H. guiarti*. In this species the early stages in the development of an " extreme " predator type of neurocranium are still preserved, the body is more slender than in *H. brownae* and the adult size is greater. Yet, it is sometimes difficult to distinguish between young *H. guiarti* and adult *H. brownae* on the superficial characters of preserved specimens. Live colours, however, provide an immediate means of separating the species. *Haplochromis guiarti* may represent an ancestral type from which the " extreme " predator group (or groups) evolved, mainly by accentuation of the syncranial characters discussed above. The nearest advanced relative of *H. guiarti* appears to be *H. bayoni*, but the skull of this species is further developed towards that of the *H. mento* type.

For the moment it is difficult to suggest the relationships of such species as *H. bartoni*, *H. estor*, *H. dentex*, *H. longirostris*, *H. mento*, and *H. macrognathus*. All bear some resemblance to one another but this is not so close as that found in the non-predator groups (see Greenwood, 1956, 1957, 1960) or amongst the subgroups of larval-embryo fish-eating species. The situation may become more amenable to analysis when the status of species like *H. taeniatus*, *H. macrodon* and *H. prognathus* is fixed. *Haplochromis prognathus* could provide an indication of a stage in the evolution of the " extreme " species. The more basic ancestral stock of this group could, on present evidence, be either the *H. guiarti*-type or the *H. serranus*-type.

Two other predator groups are more easily defined. The smaller group contains only *H. martini* and *H. michaeli*. *Haplochromis martini* retains the appearance and anatomy of a generalized species yet it is partly piscivorous in its habits (see Greenwood, 1960). *Haplochromis michaeli* is little more than an enlarged version of *H. martini* with more definitely piscivorous habits.

The second group contains three species, *H. percoides*, *H. flavipinnis* and *H. cavifrons*, which show (in that order) progressive departure from the generalized stem towards a morphological type of their own. The group is characterized by the species having oblique jaws, concave dorsal head profiles, and unique colouring and colour patterns. The pattern and, to a lesser extent, the colours of *H. percoides* and *H. flavipinnis* are related but that of *H. cavifrons* is most distinctive and unrelated. On all available evidence I consider *H. percoides* and *H. flavipinnis* to be closely related, and *H. cavifrons* to be an independent derivative from the same stem. The neurocranium in these species shows departure from the *H. guiarti* type and resembles the neurocranium of the *H. bartoni*-*H. longirostris* type. On this character, as well as the general syncranial architecture, the *H. percoides*-*H. cavifrons* group might have evolved from a species resembling *Haplochromis pellegrini*. This is an intriguing species ; it is one of the smallest predominantly piscivorous forms and its syncranium is that of the more " advanced " predators.

None of the species considered in this paper shows close relationship with the larval and embryo fish-eating species (Greenwood, 1959), a group at least diphyletic in origin.

Feeding methods. In general the fish-eating *Haplochromis* macerate their food and do not swallow it whole as do the majority of non-cichlid piscivores. The pharyngeal teeth play a major part in this process, the oral dentition serving to hold the prey during maceration. Exceptions to this generalization are those species preying on larvae and embryos, and, occasionally, those species or individuals that prey on fishes less than 15 mm. S.L.

Because the water of Lake Victoria is so murky, direct observations on feeding habits cannot easily be made. The description which follows is based entirely on aquarium studies. The species involved were *H. gowersi* (two specimens each about 22 cms. total length) as predators and small *Tilapia esculenta* and *Haplochromis* spp. (40–70 mm. total length) as prey. Live food was introduced in the *H. gowersi* tank (4 × 3 × 3 feet) whenever it was available ; otherwise the predators were fed on chopped liver or mince-meat, a diet on which they did not thrive. For some minutes after the prey was introduced, the predator remained stationary or slowly aligned itself with the prey. Then it suddenly darted forward, inevitably catching the prey fish by the caudal peduncle. Never once did I see a frontal attack. The prey struggled for a short while but soon became motionless. The predator appeared to make no further attempt to swallow its food, although slight, almost trembling jaw and opercular movements were detectable. After four or five minutes (during which the predator might swim slowly forwards) the prey fish was released. The greater part of its caudal musculature had been grated away so that the terminal vertebrae and hypurals were exposed ; the caudal fin showed less signs of damage. At this stage the prey might attempt to swim off, but usually it remained motionless. The predator then either took hold of its prey from behind, and continued to rasp away the caudal region, or it positioned itself for a frontal attack. The latter course resulted in the head and fore-part of the prey being taken into the mouth. This, of course distorted the predator's mouth and branchial region and it gulped and " chewed " vigorously for some eight to ten minutes. At the end of that time only the prey's caudal fin protruded from the jaws. In all, the process of capture and ingestion took from fifteen to twenty minutes, a lengthy business and one destroying my preconceived notions (based on *H. gowersi's* anatomy and appearance) of a fast-moving rapacious predator.

Regrettably, I do not know whether these feeding methods are general or even natural. The fact that it is unusual to find more than one fish in a predator's stomach, even when the remains of that one individual are in a state of advanced digestion, suggests that the predators feed at fairly protracted intervals. Again, the usual occurrence in any one sample of less than fifty per cent of individuals with food in the stomach seems to reinforce the idea that feeding is not a process immediately triggered off by the digestion of the last meal. For comparison, it should be noted that a comparable sample of, say, mollusc-eating or insectivorous species, would yield about eighty per cent of specimens with food in the stomach.

Prey species. Because the food is so macerated it is difficult to identify the prey species with any degree of refinement. Piecing together what identifiable remains there are, it seems that the predators described in this paper feed mainly on other Cichlidae and to a lesser extent on small Cyprinidae, generally *Engraulicypris argenteus.* The identity of the cichlids is almost impossible to ascertain beyond the generic level. The most frequent stomach contents are of *Haplochromis* ; no definite remains of *Tilapia* are recorded but one cannot be certain that *Tilapia* are not represented amongst the numerous records of " unidentifiable cichlid remains ". Against the possibility of *Tilapia* being an important element in the diet, it must be stressed that predatory *Haplochromis* are rarely encountered in the habitats favoured by *Tilapia* of a size vulnerable to *Haplochromis.* For instance, by the time young *Tilapia esculenta* leave the reed-bed " nurseries " they are too large for all but the largest individuals of any fish-eating *Haplochromis* species.

SUMMARY

(1) Sixteeen species are redescribed on the basis of new material.

(2) In addition, five new species (*Haplochromis brownae, H. nyanzae, H. bartoni, H. artaxerxes* and *H. mandibularis*) are described.

(3) With one exception (*H. brownae*) all the species are piscivorous, the principal prey being *Haplochromis.* Small cyprinids also feature in the diet, and to a slight degree, various aquatic insects. Terrestrial insects may also be eaten when, after a heavy hatch, these fall into the water.

(4) Phyletic lines and groups are less clearly defined amongst the predators than in other trophic groups. Nevertheless three major groups can be recognized.

(5) The basic predator types are considered and the anatomical specializations of the others are described.

(6) One species, *H. brownae,* is thought to represent a transitional form (in habits and anatomy) between the generalized insectivore and the basic piscivore type.

(7) Some aquarium observations on the feeding routine of *H. gowersi* are summarized.

ACKNOWLEDGEMENTS

It is with great pleasure that I thank Dr. Ethelwynn Trewavas for her advice and criticism, and for reading the manuscript of this paper. To Mr. A. C. Wheeler go my thanks for skilfully preparing the numerous radiographs on which I have based the vertebral counts. Figures 5, 9, 10, 16 and 22 are reproduced by courtesy of the Zoological Society of London.

REFERENCES

Corbet, P. S. 1961. The food of non-cichlid fishes in the Lake Victoria basin, with remarks on their evolution and adaptation to lacustrine conditions. *Proc. zool. Soc. Lond.* **136** : 1–101.

Graham, M. 1929. *A Report on the Fishing Survey of Lake Victoria,* 1927–1928, *and Appendices.* Crown Agents, London.

Greenwood, P. H. 1956. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part I. *Bull. Br. Mus. nat. Hist., Zool.* **4** : No. 5, 223–44.

—— 1957. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part II. *Bull. Br. Mus. nat. Hist., Zool.* **5** : No. 4, 76–97.

—— 1959. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part III. *Bull. Br. Mus. nat. Hist., Zool.* **5** : No. 7, 179–218.

—— 1960. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part. IV. *Bull. Br. Mus. nat. Hist. Zool.* **6** : No. 4, 227–81.

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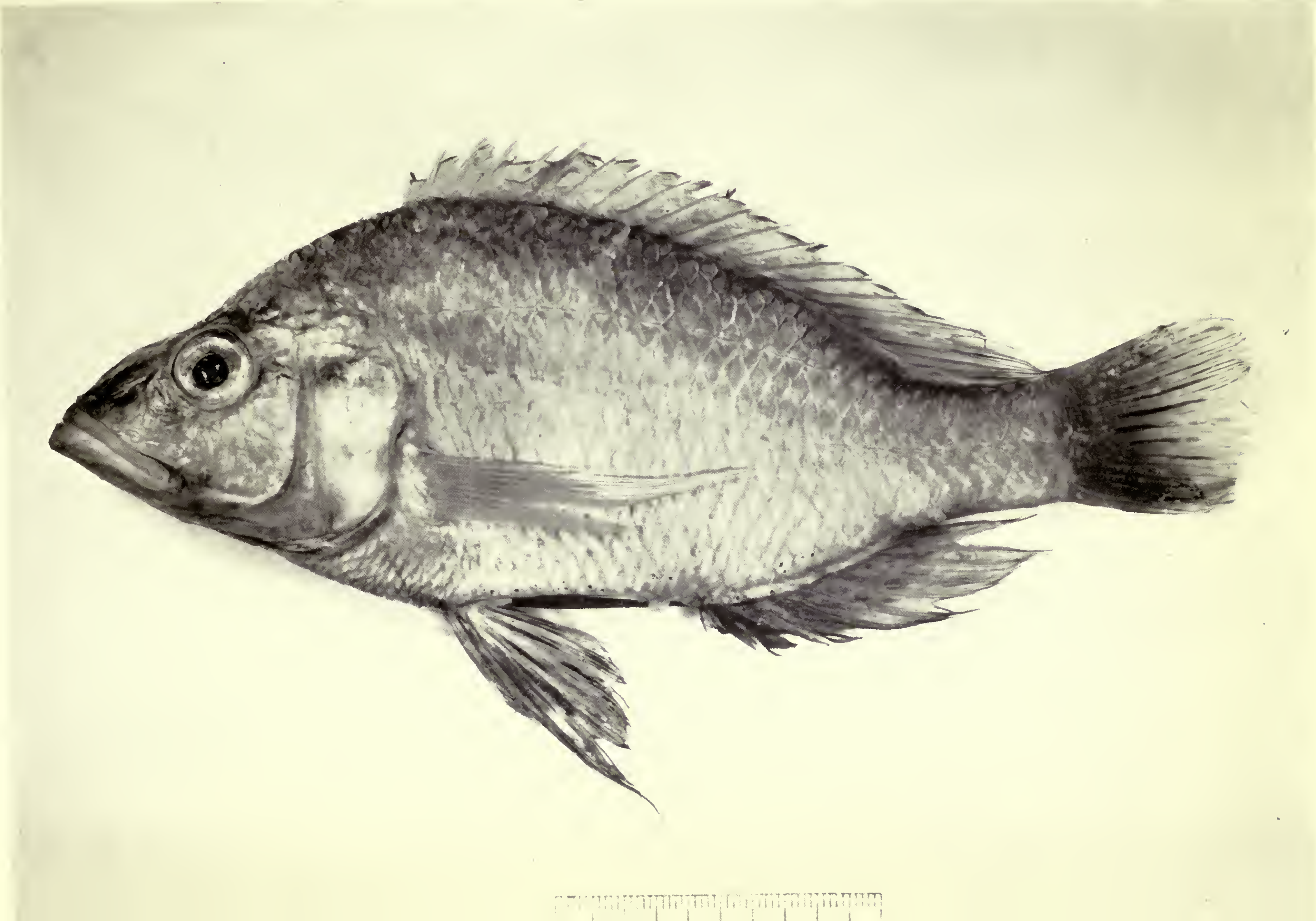
PLATE I

Haplochromis victorianus : Natural size. Photograph of a specimen compared with *H. victorianus* holotype.



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BY

ALAN SOLEM

Curator of Lower Invertebrates, Chicago Natural History Museum
Chicago, U.S.A.

Pp. 215–247 ; Plates 1–2 ; 17 Text-figures

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NOTES ON, AND DESCRIPTIONS OF NEW HEBRIDEAN LAND SNAILS

By ALAN SOLEM

A. INTRODUCTION

CURRENT knowledge of the New Hebridean land and fresh-water Mollusca was recently summarized by Solem (1959) in a study based primarily upon material in North American museum collections and a review of the previous literature. Since completion of that study in 1957, it has been possible to borrow some very important material from the British Museum (Natural History), and to obtain field collections made by Borys Malkin in 1958. Study of these collections has been long delayed and it proved impossible to devote the necessary time to reworking the numerous series of slugs. Critical examination of the shelled forms revealed four new species, including one new genus, clarified the family position of a very unusual genus (*Draparnaudia*), and added considerably to our knowledge of distribution patterns within the New Hebrides.

The British Museum (Natural History) collections are principally those made by J. R. Baker and Tom Harrisson and party in the 1920's and 1930's primarily with the Oxford University Expedition to the New Hebrides, 1933–34, and a few sets collected by L. E. Cheesman in the mid-1930's. Of particular importance was a collection of seven shells from Tatarii village, at 4,000 feet above sea level on the slopes of Mt. Tabwemasana in Western Espiritu Santo. Six specimens represented a new species of an otherwise New Zealand genus and the seventh is a new genus of a primitive helicarionid sub-family.

Borys Malkin visited several islands (Maewo, Aoba, Malekula and Vanua Lava) where the Molluscan fauna was very poorly known. Besides collecting two previously unknown species, his efforts added significantly to our knowledge of inter-island distribution. The dates of his malacological collections are : Vate Island (21st–22nd July, 1958) ; Espiritu Santo (23rd–28th, 31st July, 18th–19th, 24th–25th, August, 27th–30th September, 1958) ; Vanua Lava, Banks Group (6th–11th August, 1958) ; Maewo 29th August to 4th September, 1958). His collections are deposited in the Chicago Natural History Museum (hereafter CNHM).

ACKNOWLEDGMENTS

For kind permission to study the specimens in the British Museum (Natural History) collections, I am indebted to the Trustees of that institution. The drawings of *Phrixgnathus tatariiensis* were done by E. John Pfiffner and those of *Pseudosesara tabwemasanana* by Marion Pahl, Staff Artists at Chicago Natural History Museum ; drawings of the other shells are by Marcia Oddi, Temporary Assistant, Department of Zoology, Chicago Natural History Museum. The anatomical drawings were prepared by Miss Oddi from dissections made by the author. Drs. Yoshio Kondo and H. B. Baker have given advice concerning the systematic position of *Draparnaudia*.

B. NOTES AND DESCRIPTIONS OF SPECIES

Class *GASTROPODA*

Subclass *PULMONATA*

Superorder STYLOMMATOPHORA

Order HETERURETHRA

Superfamily SUCCINEACEA

Family SUCCINEIDAE

Genus ***SUCCINEA*** Draparnaud, 1801

Succinea (Papusuccinea) kuntziana Solem, 1959

Succinea (*Papusuccinea*) *kuntziana* Solem, 1959 : 55–58, pl. 5, figs. 1, 3–8, pl. 13, fig. 3.

Borys Malkin collected one adult under a rotting log near Luganville, Espiritu Santo (CNHM 109414). J. R. Baker and party found two adults in or near Steaming Hill Lake, Gaua, Banks Group. Apparently this species is widely distributed in the New Hebrides.

Order ORTHURETHRA

Superfamily VERTIGINACEA

Family PUPILLIDAE

Genus ***GASTROCOPTA*** Wollaston, 1878

Gastrocopta (Sinalbinula) pediculus (Shuttleworth, 1852)

Gastrocopta (*Sinalbinula*) *pediculus* (Shuttleworth) : Solem, 1959 : 58–59.

Six adults from Norovorovo, Maewo (CNHM 109351) collected by Borys Malkin add the second known New Hebridean record for this snail that has been widely dispersed by commerce.

Family ENIDAE

Genus ***RHACHISTIA*** Connolly, 1925

Rhachistia histrio (Pfeiffer, 1854)

Rhachistia histrio (Pfeiffer) : Solem, 1959 : 60–62, pl. 8, fig. 9, pl. 13, fig. 5.

Specimens in the British Museum (Natural History) collection from Vate confirm the many prior records from this island. A large series of this species was obtained by Borys Malkin on Mare, Loyalty Islands, New Caledonia (CNHM 109435, 109436). A set of these was forwarded to Dr. B. Verdcourt, East African Herbarium, Nairobi, Kenya, for comparison with African species. He has reported elsewhere (Verdcourt, 1961) that the New Hebridean–New Caledonian form is the same as the East African *Rhachidina braunsii* (von Martens), thus tending to confirm my suggestion of 1959 that *histrio* has been introduced into the Pacific Islands and Australia. Because the generic position of these shells is uncertain, I have retained the name used in my previous paper.

Subfamily DRAPARNAUDIINAE, new subfamily

Orthurethrous holopods, foot with median groove, spermatheca enlarged in basal portion, penis unforked with subapical epiphallic insertion through a large stimulatory pad. No appendages on spermatheca or penis. Radula enid with central reduced in size, bicuspid laterals and multicuspid marginals. Jaw crescent shaped with very weak striations.

It is quite difficult to know where to classify this group, since the anatomy of the Orthurethra is known to show many parallelisms and convergences. Combinations of the varying characters outlined above exclude *Draparnaudia* from most family units and certain features show strong similarities to various families. The swollen spermatheca with apical sac imbedded in the prostate is present in the European Chondrinidae, although to a lesser extent, but the radula of *Draparnaudia* is enid in character, agreeing well with those of west chinese species figured by Wiegmann (1901) Where *Draparnaudia* differs most strikingly is in the simplified penis, which is totally without any appendages or a split retractor muscle. The internal papilla of the penis is quite similar to that known for certain enids, however, and secondary reduction of the penial complexities is a common phenomenon in the Orthurethra. Few Asian or Indonesian enids have been dissected, so that forms transitional from typical enids to the simplified condition of *Draparnaudia* may well be discovered.

The amastrid-cochlicopid lines have penial appendages and the genital orifice well removed from the tentacle and near the mantle. The partulids have a shortened, triangular kidney approaching that of the Mesurethra, while the tornatellinids have the modified radula and greatly shortened uterus and prostate complex. *Draparnaudia* is thus effectively excluded by the above characters from any of the endemic Pacific Ocean orthurethran families. The usually toothed pupillids differ in the penial complexities, shortened spermatheca, uterus and prostate, and differently formed radular teeth.

The female genitalia of *Draparnaudia* is close to that of the Orculidae and Chondrinidae (see Steenberg, 1925 : pls. 2–8, particularly pl. 5), but the toothed, pupiform shell, penial complexities and varying radular structures of these groups do not indicate a close relationship. Association of *Draparnaudia* with the Enidae is based on the radula, the toothless, relatively smooth shell, and the similarity of the apical genitalia to that of the enid *Pseudochondrula*. The enlargement of the spermatheca and the simplified penis are totally unlike any enid on which data has been published, thus indicating the need for subfamily recognition of this genus.

Solem (1959 : 121) discussed previous speculations on the systematic position of *Draparnaudia* (Bulimulidae, Camaenidae) and added a third suggestion (Tornatellinidae). The present dissection of *D. lifuana* does place the genus as an orthurethran, but the family position must still be considered uncertain. Until such forms as the Timor " *Pseudonapaeus* " *apertus* (Martens), New Guinea *Apoëcus colonus* (Moellendorff) and Australian-New Guinea *Amimopina macleayi* (Brazier) are dissected, it will remain uncertain as to whether *Draparnaudia* is an isolated genus or connected to the more typical Asiatic forms by the anatomies of the above mentioned enids.

Genus *DRAPARNAUDIA* Montrouzier, 1859

Draparnaudia walkeri Sykes, 1903

Draparnaudia walkeri Sykes: Solem, 1959; 123, pl. 8, fig. 8.

Borys Malkin collected a single adult shell at Nasuli, Baldwin Bay, Espiritu Santo (CNHM 109410).

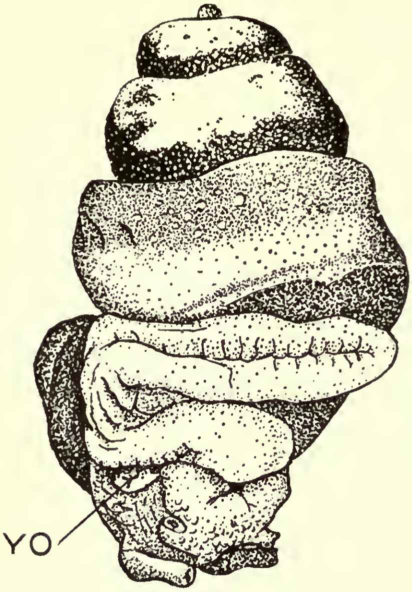
Draparnaudia lifuana Pilsbry, 1901

Text-figs. 1–7

Draparnaudia lifuana Pilsbry: Solem, 1961: 484.

Two adult, well-relaxed specimens collected by Borys Malkin at Tadine, Mare, Loyalty Islands, New Caledonia (CNHM 109411) provide the data presented above on the systematic position of *Draparnaudia*. In an attempt to pull one specimen from the shell the animal broke in two with one part remaining inside. The other shell was destroyed in order to have an entire animal for dissection. Nervous and muscular systems were not studied because of the lack of sufficient material.

Animal (Text-fig. 1) with a light buff-coloured, holopod foot. Tail rounded above, sole with a median groove, rounded posteriorly. Gonopore (YO) below and behind left ommatophoral tentacle, nearer to tentacle than to mantle collar. Pallial region (Text-fig. 2) with orthurethrous kidney (excretory pore—KO), simple and unbranched but recurved pulmonary vein. Mantle collar with simple pneumostome, no prominent lappets. Intestine opening through fold in mantle collar. Lung without secondary veining or white flecking. Apical whorls with a network of chalky white. Genitalia (Text-fig. 3) quite distinctive. Ovotestis (G) multilobate with five clumps of clavate alveoli imbedded in apical lobe of digestive gland. Hermaphroditic duct (GD) long, highly convoluted near carrefour region. Talon reduced to a short unconvoluted basal portion of hermaphroditic duct (not shown in figure) that is buried in the small albumen gland (GG). No separate carrefour region obvious, but condition of the material did not permit critical study of this region. Uterus (UT) a very thin-walled sac, swollen, without transverse folds. Free oviduct (UV) moderately long, a thin tube only moderately larger than the vas deferens (D), internally sculptured with three longitudinal rugose pilasters and a series of irregular, microscopic pilasters between the major ones. Spermatheca long, with apical sac loosely bound to prostate near to, but not reaching, the carrefour-albumen gland area. Medial portion of stalk (SS) slender, gradually becoming globosely swollen with thick muscular walls and sculptured internally (Text-fig. 4) with grooved longitudinal pilasters. Free oviduct entering laterally with a minor cluster of small pilasters radiating from the opening. Vagina (V) and spermatheca not internally differentiated, the vaginal region gradually narrowing with reduced pilaster size before junction of vagina and penial cavity to form the very short atrium (*Y*). Prostate (*DG*) a small tube bound to the uterine wall with quite numerous digitiform follicles attached to it. These tubules quite long and free of each other, variously coiled and folded. Prostate slightly shorter than uterus. Vas deferens slender, coiled around free oviduct and loosely connected by tissue to spermathecal stalk and vagina, tightly bound to atrial region. At a trial



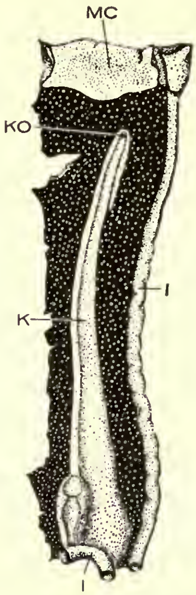


FIG. 1. *Draparnaudia lifuana* Pilsbry. Entire animal removed from shell.
YO—gonopore

FIG. 2. *Draparnaudia lifuana* Pilsbry. Pallial region.

I—intestine
K—kidney
KO—renal orifice
MC—mantle collar

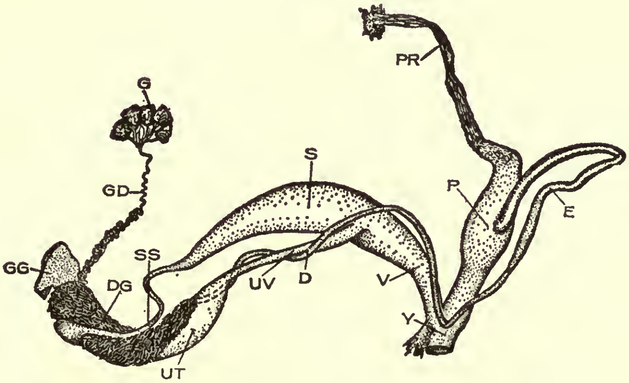
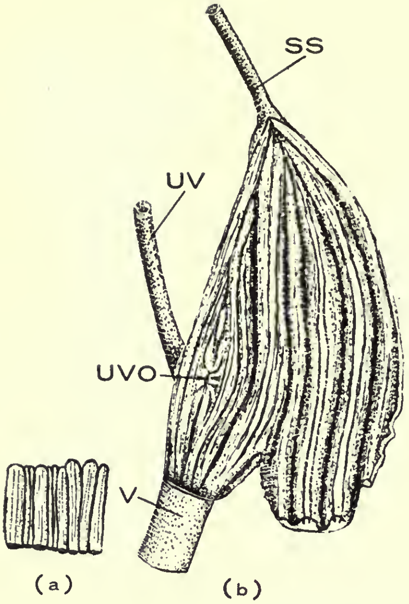


FIG. 3. *Draparnaudia lifuana* Pilsbry. Genitalia.

D—vas deferens
DG—prostate
E—epiphallus
G—ovotestis
GD—hermaphroditic duct
GG—albumen gland
P—penis
PR—penial retractor
S—spermatheca
SS—spermathecal stalk
V—vagina
UT—uterus
UV—free oviduct
Y—atrium



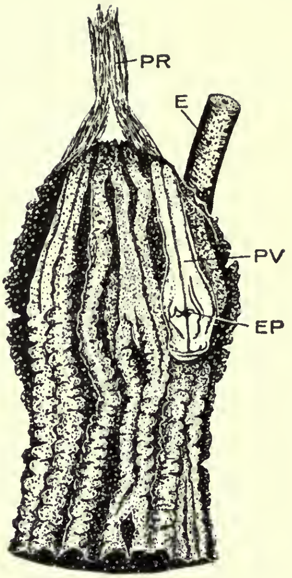


FIG. 4. *Draparnaudia lifuana* Pilsbry. Interior of spermatheca.

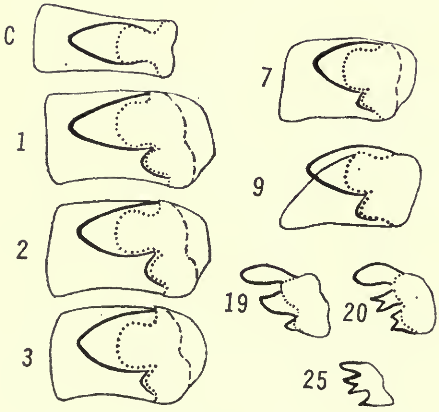
a. internal sculpture of vagina

b. vaginal region and lower spermathecal stalk

UVO—opening into vagina of free oviduct

FIG. 5. *Draparnaudia lifuana* Pilsbry. Interior of penis.

PV—penial papilla proper
EP—pore of epiphallus



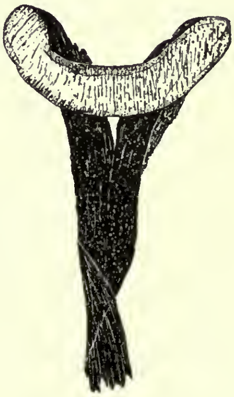


FIG. 6. *Draparnaudia lifuana* Pilsbry. Radula.

FIG. 7. *Draparnaudia lifuana* Pilsbry. Jaw.

region, one specimen had an enlarged, glandular sac, the other only a slight swelling (specimen drawn), probably indicating the break between the vas deferens proper and the epiphallus. The epiphallus ascends the penis, becoming a thick tube with muscular walls that loops around the penis and penial retractor. Epiphallus inserts subapically on the penis. Penis (*P*) with terminal retractor muscle (*PR*) that arises on the diaphragm. Penis sculptured internally (Text-fig. 5) with a series of longitudinal accessory pilasters that are simple above the point of entry of the epiphallus and corrugated below. Epiphallus enters penis through a high, grooved stimulatory pad that probably functions as a verge. Atrial region with small, smooth pilasters. Left ommatophoral retractor passing through peniovidual angle. Radula (Text-fig. 6) with 104 straight rows of teeth. Each row with unicuspid central that is distinctly smaller than the adjacent lateral, 9 to 10 bicuspid laterals with moderately squarish basal plates, and 16–17 marginals that are multicuspid because of split ectocones. Jaw (Text-fig. 7) very thin, crescent-shaped, aulacognath with very fine vertical striations.

Family PARTULIDAE

Genus ***PARTULA*** Ferussac, 1821

Partula pyramis Hartman, 1886

Partula pyramis Hartman : Solem, 1959 : 69, pl. 14, fig. 9.

A single dead specimen (CNHM 109349) was collected at 1,000 feet elevation on the trail from Karo to Amok, Malekula and a number of worn shells (CNHM 109350) on the trail from Amok-Tenmaru, Malekula by Borys Malkin. Periostracum was eroded and no sculpture or colour remained. The shells have rounded whorls of the *pyramis* type and are tentatively referred to this species.

Partula auraniana Hartman, 1888

Partula auraniana Hartman : Solem, 1959 : 70–71, pl. 15, figs. 1, 2, 6.

Borys Malkin collected shells from Vureas (CNHM 109347, juvenile), trail from Sola to Mosina (CNHM 109348, one adult, one juvenile) and at Mosina Bay (CNHM 109346, good set) on Vanua Lava, Banks Group. The large series from Mosina Bay was measured and the results of statistical treatment are summarized in Table 1. The range of variation includes part of the type set of *P. auraniana* from Aore Island (see Solem, 1959), but subspecific variation might be warranted when adequate samples from Aore are analysed.

Order SIGMURETHRA

Suborder AULACOPODA

Superfamily ARIONACEA

Family ENDODONTIDAE

Subfamily PUNCTINAE

Genus ***PHRIXGNATHUS*** Hutton, 1883

Referring two species from the New Hebrides to this New Zealand genus is supported by the discovery of a third species, described below, which has shell characters of another group of New Zealand *Phrixgnathus* and anatomy of the punctid type. Although *P. glissoni* and *P. tenuiscriptus* have the shell characters of the New Zealand group of *P. sciadium*, the new species, *P. tatariiensis*, has the shape and sculpture of the group of *P. ariel*. The microsculpture of the New Zealand and New Hebridean shells is the same, and quite different from that of the endodontinine genera of the Pacific. The anatomy of *P. tatariiensis* is punctid, thus connecting the species to the New Zealand *Phrixgnathus* and *Laoma* in animal features. Since the conchology of the New Hebridean and New Zealand shells is so similar, no hesitation is felt in leaving them in the same genus. Adequate dissections of both New Zealand and New Hebridean species might, however, result in subgeneric or generic separation.

Phrixgnathus glissoni (Ancey, 1889)

Phrixgnathus glissoni (Ancey): Solem, 1959: 81, pl. 28, figs. 3–5.

Borys Malkin found two juveniles near Luganville, Espiritu Santo (CNHM 109355) and three near adults at 1,000 feet elevation on the trail from Amok to Tenmaru, Malekula (CNHM 109354). The latter were the more trochoidal, less acutely carinated shells that Ancey called variety " B ". Local forms of *P. glissoni* may be eventually recognized, but no set larger than three shells has been examined to date, so that data are totally inadequate for any consideration of subspeciation.

Phrixgnathus tatariiensis, new species

Text-figs. 8–10, Pl. 1, figs. 1–3

Diagnosis. A small species of *Phrixgnathus* with moderately elevated spire, angulated periphery, relatively narrow umbilicus, colour markings reduced to vague radial streaks and a microsculpture of fine spiral lines crossing very low and irregular growth striae. Other New Hebridean species differ in their larger size, stronger radial ribbing, colour pattern and umbilical size. New Zealand species all present differing combinations of characters.

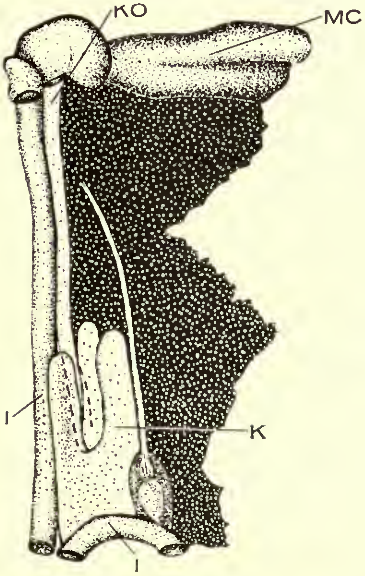
Holotype. British Museum (Natural History) No. 1961653. from Tatarii Village, 4,000 feet elevation, Western Espiritu Santo, New Hebrides. Collected by John R. Baker and party in October and November 1933.

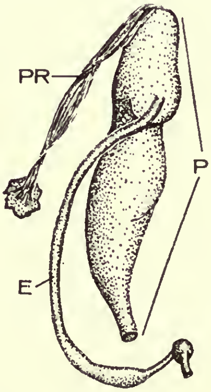
Description. Shell small, globosely turbinate with 4¼ whorls. Spire moderately elevated, not swollen, sutures lightly indented and whorls only slightly rounded. Body whorl with angulated to keeled periphery located well above mid-point. Surface of shell with a distinct sheen and microsculpture of very fine incised spiral lines crossing very low and irregular growth striae. Colour corneus with vague, irregular radial reddish yellow streaks. Umbilicus open, narrow, contained 11–13 times in the diameter with slight constriction due to expansion of the basal lip. Aperture without teeth and lip simple. Diameter of holotype 3·5 mm., height 2·38 mm.

Animal with aulacopod foot, bilobed sigmurethrous kidney, typically punctid teeth and jaw. Male genitalia with apical insertion of penial retractor, subapical entrance of epiphallus (?) and heavily pilastered penis. Other aspects of anatomy not studied.

Paratypes. British Museum (Natural History) No. 1961654 and Chicago Natural History Museum No. 110859 from the type set.

Discussion. The animals had retracted into the shell before death and the shell had been almost completely decalcified in the preservative. It was thus necessary to destroy the shell during dissection of the soft parts and great care had to be exercised in the handling of the very fragile specimens. The degree of retraction and condition of the soft parts rendered dissection quite difficult and only features of the gross morphology could be observed. Other than jaw and dentition, no other aspect of laomid anatomy has been recorded and the meagre results obtained here provide very important data about their classification. The pallial region is of the same type found in the Holarctic *Punctum* (Pilsbry, 1948, p. 642, fig. 349*e*), possessing the quite peculiar bilobed sigmurethrous kidney (Text-fig. 8). The radular teeth are typically punctid. The jaw is composed of numerous rhombic plates that are very loosely connected by a thin membrane. The male genitalia (Text-figs. 9, 10) have a complex internal pilaster system, probably associated with spermatophore formation. In one of the two animals dissected, a large, muscular spermatophore was present in the lower part of the penis. The subapical insertion of the epiphallus clearly separates *Phrixgnathus* from *Punctum*, although other anatomical features are similar.





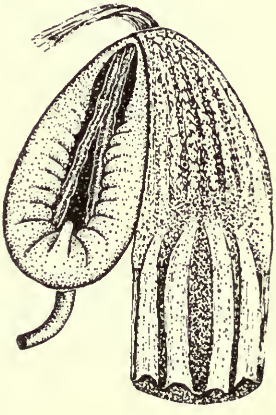


FIG. 8. *Phrixgnathus tatariiensis.* Pallial region.
FIG. 9. *Phrixgnathus tatariiensis.* Male genitalia.
FIG. 10. *Phrixgnathus tatariiensis.* Interior of penis

The shell of *P. tatariiensis* (Pl. 1, figs. 1–3) is perhaps most similar in shape to the New Zealand *P. subariel*, obviously differing in umbilicus, sculpture, colour pattern and degree of keeling. The colour pattern is more reduced than in any *Phrixgnathus*, approaching some of the *Paralaoma* in tonal quality. Sculpture was about as in *P. celia*.

Subfamily Endodontinae

Genus *MOCELLA* Iredale, 1915

Mocella euryomphala Solem, 1959

Mocella euryomphala Solem, 1959 : 83–85, pl. 6, figs. 7–8, pl. 31, figs. 1–5.

Specimens collected at Norovorovo, Maewo (CNHM 109384) by Borys Malkin and on Gaua, Banks Group by J. R. Baker in 1928 show no important differences from paratypes of this Espiritu Santo species and indicate that it is widely distributed in the New Hebrides.

Superfamily Limacacea

Family Helicarionidae

Subfamily Euconulinae

Genus *CONEUPLECTA* Moellendorff, 1893

Coneuplecta (Sitalina) microconus (Mousson, 1865)

Coneuplecta (*Sitalina*) *microconus* (Mousson) : Solem, 1959 : 94–95, pl. 34, fig. 10.

Borys Malkin found specimens at Bankaharijitoa, 1,500–2,000 feet elevation, above Dunduy, Aoba (CNHM 109377) and J. R. Baker collected it on Gaua and Espiritu Santo. A common species widely dispersed by human agency.

Subfamily Microcystinae

Genus *LIARDETIA* Gude, 1913

Liardetia (Liardetia) samoensis (Mousson, 1865)

Liardetia (*Liardetia*) *samoensis* (Mousson) : Solem, 1959 : 96–97, figs. 3, *d–f*, pl. 33, figs. 4–6.

New island records are provided by shells from 500 feet elevation above Nasaua, Maewo (CNHM 109383) and on the trail from Sola to Mosina, Vanua Lava, Banks Group (CNHM 109376). This is another species spread by commerce.

Subfamily Sesarinae

This primitive helicarionid subfamily was previously represented in the New Hebrides by two genera, *Orpiella* and *Dendrotrochus*. A single shell collected by J. R. Baker in 1934 at Tatarii Village, 4,000 feet elevation on the slopes of Mt. Tabwemasana, Espiritu Santo (see Baker, 1935 for a description of the area) proved to be a new species and genus, related anatomically to *Dendrotrochus*, but having quite primitive shell characters. It is described below as *Pseudosesara tabwemasanana*.

Genus *ORPIELLA* Gray, 1855

Orpiella (Halozonites) retardata depressa Solem, 1959

Orpiella (*Halozonites*) *retardata depressa* Solem, 1959 : 100–101, pl. 34, figs. 4–6.

Borys Malkin collected shells from near Luganville, Espiritu Santo (CNHM 109381) and nearly adult shells from the trail between Karo and Amok, Malekula (CNHM 109382).

Genus ***DENDROTROCHUS*** Pilsbry, 1894

Dendrotrochus (Santotrochus) eva eva (Pfeiffer, 1853)

Dendrotrochus (*Santotrochus*) *eva eva* (Pfeiffer) : Solem, 1959 : 102–103, pl. 10, fig. 13, pl. 25, figs. 1, 2.

There is considerable variation in size, shape, colour pattern and degree of carination. Material collected by Malkin & Baker extend both the geographical range and the known range of shell variation. A set of sixteen shells from " Vate Island " collected by Baker in 1926 had eleven unbanded, four with wide spiral bands and one with a narrow spiral band. The six adults were 9·1–11·0 mm. high, 12·2–15·2 mm. in diameter, h/d ratio 0·70–0·75, with $5\frac{1}{8}$–$5\frac{5}{8}$ whorls. A single individual from the waterfall on the Boofa R., Vate collected by J. R. Baker in 1922 was 11·8 mm. high, diameter 13·9 mm., h/d ratio 0·85, with $6\frac{1}{4}$ whorls. The whorl count and h/d ratio of this specimen are the greatest yet known for *D. eva eva*, and approach the measurements of *D. layardi*.

Borys Malkin collected juveniles at 1,000 feet elevation on the trail from Karo-Amok, Malekula (CNHM 109357) and at 1,500–2,000 feet elevation at Bankaharijitoa above Dunduy, Aoba (CNHM 109358). Both juveniles (CNHM 109359) and an adult (CNHM 109360) were taken at 500–800 feet elevation near Nasaua, Maewo, and one dark brown adult with a sharp keel was collected at Norovorovo school above the village, Maewo (CNHM 109361). Previously, this race was known only from Epi and Vate Islands.

Dendrotrochus (Santotrochus) eva stramineus Sykes, 1903

Dendrotrochus (*Santotrochus*) *eva stramineus* Sykes : Solem, 1959 : 103–104, pl. 10, fig. 14, pl. 25, figs. 3–5.

Borys Malkin found a single sub-adult shell at Vureas, Vanua Lava, Banks Group (CNHM 109362). Like other reported Banks' shells, it was without any colour band and relatively small in size. Possibly the Banks' populations are subspecifically separable.

Dendrotrochus (Santotrochus) layardi (Hartman, 1889)

Dendrotrochus (*Santotrochus*) *layardi* (Hartman) : Solem, 1959 : 105–106, pl. 6, figs. 5, 6, pl. 7, figs. 3, 4, pl. 25, figs. 6–9.

In 1929 J. R. Baker collected specimens from Toneva and East Central Espiritu Santo. The latter were quite depressed for this species. but had the typical colour patterns. Borys Malkin found a few examples near Luganville (CNHM 109363), and at Baldwin Bay, Espiritu Santo (CNHM 109365).

Genus ***PSEUDOSESARA***, new genus

Shell depressed, body whorl angulated, whorls about four, flattened above with spire only moderately elevated. Umbilicus open but minute. Apical whorls with extremely delicate radial riblets. Post apical whorls with very fine numerous radial riblets between moderately high, lamellate radial ribs that terminate slightly below the periphery. Major ribs 40 on last whorl. Base of shell smooth, shining with faint subperiostracal radial lines. Colour light buff. Normal condition of lip unknown.

Animal aulacopod with well defined pedal grooves and a tripartite sole. Mantle lappets, caudal areas, apical portions not observed. Radula with tricuspid central tooth, bicuspid laterals and multicuspid marginals with long basal plates. Epiphallus with distinct lime sac, penial retractor inserted near mid-point of epiphallus, penis sheath absent. Penial cavity (Text-fig. 13) with central sac-like penis flanked by two large stimulatory pads. Spermatophore unknown.

Type species.—*Pseudosesara tabwemasanana*, new species

The single known specimen of *Pseudosesara* had been preserved in an acidic solution at one time, so that calcareous portions of the shell were either dissolved or seriously weakened. Lip and basal portion of the body whorl were missing upon receipt of the collection for study, and the rest of the shell cracked in several places. The animal had completely withdrawn into the shell before death. The slightest handling resulted in further damage to the specimen, and, after preparing detailed drawings, the last whorl was sacrificed in order to study portions of the anatomy. The shell alone could not indicate family position, yet full study of the anatomy could be made only by destroying the entire shell.

A compromise was attempted, with the first $3\frac{1}{4}$ whorls remaining intact, and the lower portion of the animal cut off and dissected. The multicuspid radular marginals (Text-fig. 14) with long basal plates, aulacopod foot with tripartite sole, sigmurethrous kidney (Text-fig. 11), epiphallic lime sac and lack of additional accessory amatorial organs, place *Pseudosesara* as a member of the helicarionid subfamily *Sesarinae*.

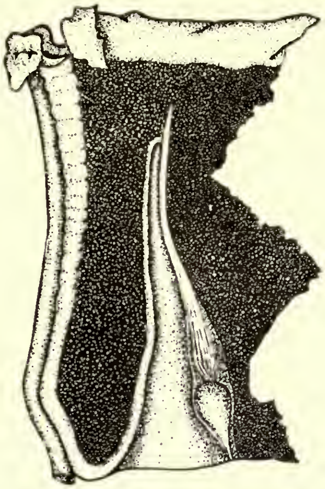
The shell differs from the other Pacific Island sesarine genera (*Orpiella* and *Dendrotrochus*) by its depressed form with angulated periphery, strong radial ribbing above and minutely open umbilicus. In these characters it superficially resembles the Burmese-Indian genus *Sesara*, hence the generic name *Pseudosesara* for the New Hebridean species. *Sesara* differs in having an often lamellate aperture and in numerous anatomical details, but there is a basic conchological similarity. *Orpiella* differs in having a penis sheath, lacking a vergic papilla, and in having a smooth shell with a closed umbilicus. *Dendrotrochus* differs in having the penial retractor inserted at the junction of the penis and epiphallus, a quite different pilaster arrangement in the penis, and in the only superficially perforated, rib-striated, conical shell.

Probably differences will be found in the structures of the more apical genitalia, but only terminal portions (Text-fig. 12) could be examined in the present study.

Pseudosesara tabwemasanana, new species

(Text-figs. 11–14, Pl. 1, figs. 4–6)

Diagnosis. A depressed helicoid shell with $4\frac{1}{8}$ flattened whorls, an angulated periphery, radial ribs that are relatively widely spaced and terminate just below the periphery, with a smooth, shining base. Umbilicus minute, contained 18 times in the diameter. Animal a typical sesarine helicarionid with the penial retractor inserting



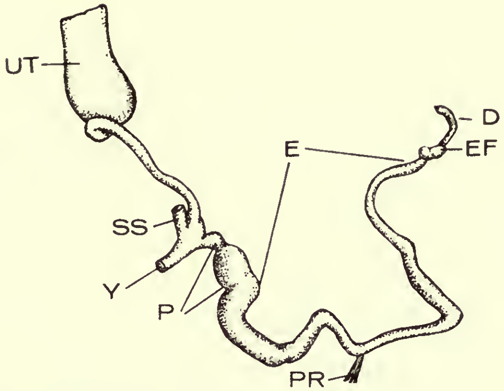

UT
D
E
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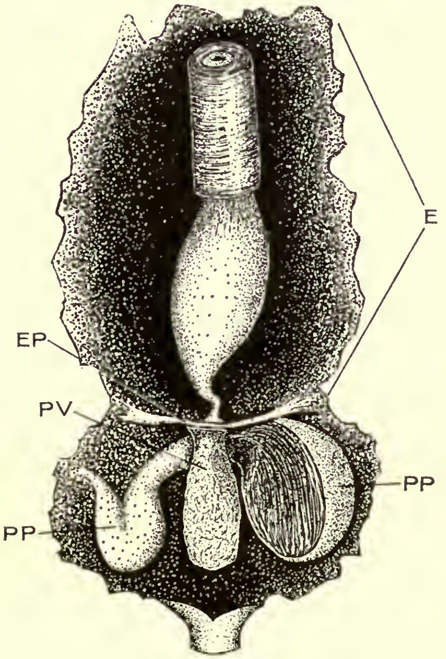
FIG. 11. *Pseudosesara tabwemasanana.* Pallial region.

FIG. 12. *Pseudosesara tabwemasanana.* Genitalia.
EF—epiphallic flagellum



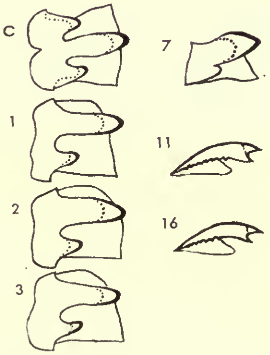


FIG. 13. *Pseudosesara tabwemasanana.* Interior of penis.
PV—penial verge
PP—penial papilla

FIG. 14. *Pseudosesara tabwemasanana.* Radula.

near the mid-point of the epiphallus and the small, globose penial cavity containing a finger-shaped sac-like penis flanked by two large stimulatory pads.

Holotype. British Museum (Natural History) No. 1961655 from Tatarii Village, 4,000 feet elevation, Western Espiritu Santo, New Hebrides. Collected by John R. Baker and party in October and November 1933.

Description. Shell depressed helicoid with $4\frac{1}{8}$ relatively flattened whorls. Body whorl angulated but not keeled. Apical whorls $1\frac{5}{8}$, very minutely radially ribbed. Remaining whorls with rather widely spaced (40 on body whorl), lamellate radial ribs that just cross the periphery, and a microsculpture of very fine radial threads between the major ribs. Base of shell smooth and shining with faint subperiostracal radial lines visible under magnification. Umbilicus open, contained 18 times in the diameter. Colour light buff with the tops of the ribs whitish. Lip broken and normal adult condition unknown. Diameter of holotype 10·82 mm., height 5·40 mm.

Animal with typical aulacopod grooves, tripartite sole with central portion narrower than the lateral areas. Pallial region (Text-fig. 11) sigmurethrous with quite elongated narrow kidney and closed secondary ureter. Terminal genitalia (Text-fig. 12) sesarine with distinct lime sac (*EF*) at terminus of epiphallus (*E*), penial retractor (*PR*) inserting slightly below mid-point of epiphallus, penis proper (*P*) small and globose, atrial opening (*Y*), spermathecal stalk (*SS*) and basal portion of uterus (*UT*) only other portions extracted. Internal structure of penis and lower epiphallic portion (Text-fig. 13) with a diaphragm (*EP*) separating the chambers of epiphallus and penis. The epiphallus is a heavy muscular tube terminating in a more glandular, thin-walled sac leading to a small tubule that passes through the diaphragm into the finger-like, thin, collapsed penis. There are two stimulatory pads: a large dished hemisphere whose base is anchored to the diaphragm and whose body lies free in the cavity and a smaller, U-shaped pad attached to the wall of the penial cavity with the base of the " U " elevated and quite swollen. Radula with 84 rows, formula 45–7–1–7–45. Teeth (Text-fig. 14) typical of family in cusp structure, distinctive only in the comparatively wide basal plates of the central and lateral teeth.

Remarks. Pseudosesara tabwemasanana cannot be mistaken for any other New Hebridean shell. The ribs terminating just below the periphery, minute umbilicus and microsculpture sufficiently characterize the species. In general appearance it could be mistaken for an endodontid, but its anatomy clearly establishes its place in the Sesarinae.

Family ZONITIDAE

Subfamily TROCHOMORPHINAE

Genus **TROCHOMORPHA** Albers, 1850

Trochomorpha (Hartmanitrochus) rubens (Hartman, 1888)

Trochomorpha (*Hartmanitrochus*) *rubens* Hartman: Solem: 1959: 109–113, pl. 6, figs. 1, 2, 4, pl. 24, figs. 1–11, 14.

Material examined for my earlier study suggested an ecological separation into *rubens* (ground) and *convexa* (tree) under undisturbed conditions, with hybridization occurring under plantation ecology. No further data on this hypothesis are provided by material examined in this study, but several new locality records are added. J. R. Baker in 1929 collected specimens of form *rubens* at Mt. Touri and in East Central Espiritu Santo. In 1936 Miss L. E. Cheesman found the same form at Ounua, Malekula. Borys Malkin made collections at Luganville, Espiritu Santo (CNHM 109369) and Nasuli, Baldwin Bay, Espiritu Santo (CNHM 109368). Specimens from 500–800 feet elevation above Nasaua, Maewo, New Hebrides (CNHM 109370) add a new island record. Fewer specimens were obtained of form *convexa* : some from Luganville, Espiritu Santo (CNHM 109372) and a set from 1,500–2,000 feet elevation at Bankaharijitoa above Dunduy, Aoba (CNHM 109373). The latter are a new island record and in shape correspond most closely to those figured by Solem (1959 : pl. 24, fig. 8).

Trochomorpha (Hartmanitrochus) bakeri Solem, 1959

Trochomorpha (*Hartmanitrochus*) *bakeri* Solem, 1959 : 113–114, pl. 24, figs. 13, 15–17.

A single specimen from the edge of Steaming Hill Lake, Gaua, Banks Group collected in 1933 by T. Harrisson is tentatively referred here. It is 15·3 mm. in diameter, 7·6 mm. high with $5\frac{1}{8}$ whorls. The spiral colour band is wider and nearer the suture than in most specimens of *bakeri*, but it is nearer to *bakeri* than to *rubens* in colour. Preservation in formalin had eroded the surface sculpture. In some respects the Gaua shell is intermediate between *bakeri* and the Quoy and Gaimard Vanikoro specimen figured in Solem (1959 : pl. 12, figs. 3–5).

Suborder HOLOPODA

Superfamily ACHATINACEA

Family SUBULINIDAE

Genus ***SUBULINA*** Beck, 1837

Subulina octona (Bruguière, 1792)

Subulina octona (Bruguière) : Solem, 1959 : 118.

Records of this widely introduced snail are : near Luganville, Espiritu Santo ; Vila and Devil's Point, Vate ; Tenmaru and the trail from Karo to Amok at 1,000 feet, elevation Malekula ; and Vureas and trail from Sola to Mosina, Vanua Lava, Banks Group (all Borys Malkin collections).

Genus ***OPEAS*** Albers, 1850

Opeas pumilum (Pfeiffer, 1840)

Opeas pumilum (Pfeiffer) : Solem, 1959 : 118–119.

J. R. Baker's material included examples from Vate and Gaua, Bank's Group. Borys Malkin found it at Vila and Devil's Point, Vate ; Luganville, Espiritu Santo ; Norovorovo, Maewo ; and the trail from Karo to Amok, Malekula. At the two localities on Vate and on Espiritu Santo it was collected wih *Subulina octona* ; at Norovorovo, Maewo with *Lamellaxis gracilis*.

Genus *LAMELLAXIS* Strebel and Pfeffer, 1882

Lamellaxis (Allopeas) gracilis (Hutton, 1834)

Lamellaxis (*Allopeas*) *gracilis* (Hutton) : Solem, 1959 : 119.

In 1934 specimens were taken near Steaming Hill Lake, Gaua, Bank's Group by T. Harrisson. Borys Malkin collected a good series near Norovorovo, Maewo.

Family EULOTIDAE

Following an earlier usage of Pilsbry, Solem (1959) adopted the name Bradybaenidae for this taxon. H. B. Baker (1959) indicated that it should probably be called Eulotidae and his suggestion is followed here.

Genus *BRADYBAENA* Beck, 1837

Bradybaena similaris (Ferussac, 1821)

Shells collected on Vate by J. R. Baker and near Luganville, Espiritu Santo, only confirm earlier records of this introduced species.

Superfamily BULIMULACEA

Family BULIMULIDAE

Subfamily BULIMULINAE

Genus *PLACOSTYLUS* Beck, 1837

Placostylus (Poecilocharis) bicolor (Hartman, 1889)

Placostylus (*Poecilocharis*) *bicolor* (Hartman) : Solem, 1959 : 136–137, pl. 12, figs. 6–9, pl. 22.

Three shells with the soft parts preserved were collected by T. Harrisson on "Espiritu Santo" without further localization. Dissection of the soft parts suggested that use of the subfamily Placostylinae should be abandoned and *Placostylus* and *Diplomorpha* are here considered to belong to the subfamily Bulimulinae. Results of the anatomical study will be published elsewhere.

Genus *DIPLOMORPHA* Ancey, 1884

Diplomorpha (Diplomorpha) layardi Ancey, 1884

Diplomorpha (*Diplomorpha*) *layardi* Ancey : Solem, 1959 : 138–141, pl. 23, figs. 7–12.

Miss L. E. Cheesman in 1936 collected a few small adults at Vila, Vate. Borys Malkin found a small adult and several juvenile shells under stones at Tenmaru, Malekula and collected a good series at 1,000 feet elevation on the trail from Karo to Amok, Malekula from ground litter (CNHM 109474). The size and shape variation of the latter set is summarized in Table 1. There is virtually no difference in measurements from the Vate populations studied by Solem (1959).

Diplomorpha (Diplomorpha) peasei (Cox, 1871)

Diplomorpha (*Diplomorpha*) *peasei* (Cox) : Solem, 1959 : 141–142, pl. 19, fig. 15.

Previously there was great uncertainty as to the exact locality of this species. Aoba (=Omba) and Aore were the suggested possibilities with Aore seeming the more probable of the two. Borys Malkin, however, collected a large set between 1,500–2,000 feet elevation at Bankaharijitoa above Dunduy, Aoba (CNHM 109475) providing the first definite record. Size and shape variation are summarized in Table 1. There are no significant differences from *D. delautouri* in size, shape or whorl count, *D. peasei* being characterized only by its larger umbilicus and slightly more expanded body whorl. Possibly only subspecific differentiation is involved, but until further records are known, it seems best to treat them as distinct.

Diplomorpha (Diplomorpha) delautouri (Hartman, 1886)

Diplomorpha (*Diplomorpha*) *delautouri* (Hartman) : Solem, 1959 : 142–144, pl. 19, fig. 14, pl. 23, figs. 1–6.

Borys Malkin found one average sized adult near Luganville, Espiritu Santo (CNHM 109399) and two quite large specimens from Tasmalune, Espiritu Santo (CNHM 109402). The latter measure :

h	d	h/d ratio	Whorls
30·4	20·6	1·47	5
28·4	18·3	1·55	5

making them the largest known individuals of this species.

Diplomorpha (Quiros) bernieri (Hartman, 1890)

Diplomorpha (*Quiros*) *berneiri* (Hartman) : Solem, 1959 : 145–147, pl. 21, figs. 7–8.

Several examples of form *ruga* were collected on " Espiritu Santo " by J. R. Baker in 1925 and preserved in alcohol. Dissection of these did not reveal any significant differences from the anatomy of the typical subgenus. Conchological features, however, suggest that *Quiros* be retained as a valid subgrouping.

Superfamily STREPTAXACEA

Family PARYPHANTIDAE

Genus ***DELOS*** Hutton, 1904

Delos (Hebridelos) rapida (Pfeiffer, 1853)

Delos (*Hebridelos*) *rapida* (Pfeiffer) : Solem, 1959 : 153–154, pl. 11, figs. 1–3.

J. R. Baker in 1925 collected a few specimens on Vate Island.

Genus ***OUAGAPIA*** Crosse, 1894

Ouagapia santoensis Solem, 1959

Ouagapia santoensis Solem, 1959 : 160–161, pl. 28, figs. 6–8.

A single shell from Espiritu Santo collected by J. R. Baker is 7·0 mm. in diameter with 4¼ whorls. This is the largest known specimen of this species.

Ouagapia perryi (Smith, 1897)

(Pl. 2, figs. 1–3)

"*Charopa*" *perryi* Smith : Solem, 1959 : 88–89.

Examination of a paratype from Rotuma Island (B.M. 97.11.8.55) enabled the following redescription to be drawn :

Shell small, solid, widely umbilicated, spire but slightly elevated. Whorls a little less than four, increasing rapidly in width, moderately flattened laterally, with deeply impressed sutures. Apical whorl smooth (eroded), remaining whorls with retractively curved radial ribs which become markedly sinuate on the body whorl. No trace of spiral or microsculpture between the radials. Sculpture heavy on base of shell and continued into umbilicus. Body whorl moderately deflected, aperture ovate with heavy parietal callus. Umbilicus very wide, contained 2·75 times in the diameter. Wall of umbilicus rounded, but not keeled. Diameter 3·4 mm., height 1·97 mm.

New figures are presented in order to clarify its position. In sculpture, whorl increment and shape, colour and nuclear characters, *Ouagapia perryi* is very similar to the Tongan and Samoan Islands *Ouagapia gradata* complex, but differs significantly in having heavy radial sculpture in the umbilical region, a complete lack of spiral impressed lines and a rounded (not keeled) umbilical shoulder. The New Guinea-Bismarck-Queensland group of *O.* (*Torresiropa*) *spaldingi* differs in having a wider umbilicus with keel, a peripheral keel and reduced sculpture. None of these have been adequately studied as to anatomy and the division of *Ouagapia* into smaller phyletic units is not yet possible.

In 1925 J. R. Baker collected a single shell on Gaua, Banks Islands that measured 4·12 mm. in diameter, 2·06 mm. high with $3\frac{5}{8}$ whorls. In comparison with the Rotuma paratype the width of the whorls increases at a more rapid rate. Until careful comparisons can be made of the Gaua shell, the Mota Island, New Hebrides holotype and the Rotuma paratypes it cannot be certain that only one species is involved. For the present, however, I prefer to use the name *perryi* to cover all three populations.

Superorder BASOMMATOPHORA

Superfamily LYMNACACEA

Family PLANORBIDAE

Genus **PHYSASTRA** Tapparone-Canefri, 1883

Physastra layardi (Ancey, 1905)

Physastra layardi (Ancey) : Solem, 1959 : 163–164.

It must be emphasized that the name *layardi* is used only for the sake of convenience, since the New Hebridean populations are conspecific with New Caledonian forms, and, possibly, Fijian and Tongan populations belong to the same species. Until this can be determined and the nomenclature untangled, it seems best to use a name based on New Hebridean shells for the New Hebridean population.

J. R. Baker collected specimens from Steaming Hill Lake, Gaua, Banks Group in both shallow water and dredged from 30 feet deep. Both lots were juvenile, but compared well with young shells from the Espiritu Santo populations. Borys Malkin found dead adults and live young at Devil's Point, Vate; a dead adult in drift at Nasuli, Baldwin Bay, Espiritu Santo; and live adults in a muddy stream one mile south of Nasaua, Maewo.

Genus *GYRAULUS* Charpentier, 1837

Gyraulus (Gyraulus) montrouzieri (Gassies, 1863)

Gyraulus (*Gyraulus*) *montrouzieri* (Gassies): Solem, 1959: 164–166, pl. 33, figs. 10–12.

Borys Malkin collected six adults and several subadults at Devil's Point, Vate. J. R. Baker found three young shells on Gaua, Banks Group, one of which is typical *montrouzieri*, while the other two seem nearer to the New Caledonian *G. rossiteri* (Crosse) but are too young for positive identification.

Subclass *PROSOBRANCHIA*

Order ARCHAEOGASTROPODA

Superfamily NERITACEA

Family HELICINIDAE

Genus *PLEUROPOMA* Moellendorff, 1893

Pleuropoma albescens (Hartman, 1890)

Pleuropoma albescens (Hartman), Solem, 1959: 172–173, pl. 26, figs. 5–7, 11.

Typical specimens were collected by Borys Malkin at Baldwin Bay, near Luganville, and at Nasuli on Baldwin Bay, Espiritu Santo. J. R. Baker's collections contained many specimens from Mt. Touri and East Central Espiritu Santo. The last two collections contained a few individuals of *P. sublaevigata* mixed with the *P. albescens*, while Malkin's sets were more evenly balanced in number of individuals.

Pleuropoma sublaevigata (Pfeiffer, 1852)

Pleuropoma sublaevigata (Pfeiffer): Solem, 1959: 173–175, pl. 10, figs. 1–3, pl. 26, figs. 12, 13.

This common and widely distributed New Hebridean species was found on Gaua, Vate (Vila) and Espiritu Santo (Mt. Touri and East Central) by Baker and Cheesman. Borys Malkin collected it on Espiritu Santo (Nasuli, near Luganville, and Baldwin Bay), Aoba (Lolowai), Maewo (at 500–800 feet elevation above Nasaua, and Nororovorovo School above the village), Malekula (trail from Karo to Amok at 1,000 feet elevation, and Tenmaru), and in the Banks Group on Vanua Lava (Vurass, trail from Sola to Mosina, and Mosina Bay).

The Malekula and Vanua Lava shells were relatively small, about the same size as the Espiritu Santo populations. Those from Maewo and Aoba were appreciably larger, approaching the size of *Helicina novella* Mabille, 1895, which I had tentatively considered to be a synonym based on large individuals of *P. sublaevigata*. The types of *novella* are unknown, but the presence of populations with larger individuals of *P. sublaevigata* suggests that the proposed synonymy may be correct.

Time did not permit sexing of the numerous specimens and detailed analysis of size and shape variation.

Pleuropoma articulata (Pfeiffer, 1854)

Pleuropoma articulata (Pfeiffer) : Solem, 1959 : 176–177, pl. 10, figs. 7–9.

J. R. Baker collected specimens from Vate and Gaua. The largest specimen from Vate was 6·08 mm. in diameter, 4 mm. high with $4\frac{3}{4}$ whorls, which greatly exceeded the size of the largest previously reported shell of this species (see Solem, 1959 : p. 171, Table XII). Borys Malkin collected several individuals at Tenmaru, Malekula (CNHM 109455).

Genus ***CERATOPOMA*** Moellendorff, 1893

Ceratopoma draytonensis (Pfeiffer, 1857)

Helicina draytonensis Pfeiffer, 1857, *Proc. Zool. Soc. London*, **1856** : 392—Drayton Range, North Australia ; Sowerby, 1866, *Thes. Conch.*, **3** : 286, pl. 271, figs. 199–200 ; Cox, 1868, *Monog. Austr. Land Shells*, p. 106, pl. 17, fig. 13.

Helicina diversicolor Cox, 1866, *Proc. Zool. Soc. London*, **1866** : 375—Pine Mt., Ipswich, Queensland ; Cox, 1868, *Monog. Austr. Land Shells*, pp. 105–106, pl. 17, fig. 9.

Palaeohelicina (*Ceratopoma*) *diversicolor* (Cox) : Wagner, 1911, *Syst. Conch. Cab.*, I, 18, (2), p. 262, pl. 52, figs. 5–7 (very poor).

Ceratopoma draytonensis (Pfeiffer) : Iredale, 1937, *Austr. Zool.*, **8**, (4), p. 293.

Two specimens collected by Borys Malkin at 500–800 feet elevation above Nasaua, Maewo (CNHM 109458) are totally different from any previously known New Hebridean helicinid. Their smooth, shining surface, callus and configuration of the umbilical lip are the same type found in the Australian *Ceratopoma*. Comparison with available material showed that it was nearly identical with a Port Curtis, Queensland specimen (CNHM 28556) that was labelled *C. gladstonensis* (Cox), but agrees closely with the type figures of *draytonensis*.

The synonymy cited above is taken from the literature, since I did not have sufficient material to enable study of the limits of variation in the Australian species of *Ceratopoma*. The specific designation is uncertain, but I have no hesitation in considering that the New Hebridean shell is an Australian *Ceratopoma* that has been accidentally introduced into the New Hebrides, probably on plants. Other possible New Hebridean-Australian imports are discussed by Solem (1959), so that this does not seem to be an isolated case.

Order MESOGASTROPODA

Suborder ARCHITAENIOGLOSSA

Superfamily CYCLOPHORACEA

Family POTERIIDAE

Solem (1959) discussed the probable relationships of *Ostodes*, *Gonatoraphe* and *Gassiesia*. The male and female organs of the first two genera were briefly discussed, but no data was available on *Gassiesia*. Borys Malkin collected a single small male of *Gassiesia couderti* (Fischer & Bernardi) from Kuto, Ile des Pins, New Caledonia (CNHM 109427). The mid-dorsal verge has a closed seminal groove and a very long terminal appendage, about twice the length of that found in the New Hebridean *Gonatoraphe fornicata*. *Gassiesia* thus is nearer to *Gonatoraphe* in vergic structure than to the Samoan *Ostodes*.

Genus ***GONATORAPHE*** Moellendorff, 1898

Gonatoraphe fornicata (Pfeiffer, 1854)

Gonatoraphe fornicata (Pfeiffer) : Solem, 1959 : 183–185, pl. 6, figs. 9–10, pl. 9, figs. 4–6, pl. 26, figs. 1–2.

J. R. Baker in 1925 found very small juvenile shells on Vate. Borys Malkin collected large adults at Tasmalune, Espiritu Santo (CNHM 109424) ; juvenile shells at Tenmaru, Malekula (CNHM 109426) and at 500–800 feet elevation above Nasaua, Maewo (CNHM 109425) ; and relatively small adults at 1,000–1,500 feet elevation at Bankaharijitoa above Dunduy, Aoba (CNHM 109423).

Family PUPINIDAE

Subfamily PUPININAE

Genus ***PUPINA*** Vignard, 1829

Solem (1959, pp. 186–189) briefly discussed the classification of the Pupininae and suggested that most of the genera proposed by Clench (1949) be reduced to sectional or subgeneric ranking. In the Solomons and New Hebrides, Clench (loc. cit.) recognized two genera, distinguished by the presence (*Pupina*) or absence (*Kanapa*) of an apertural notch. Solem (1959, p. 189) recorded variation in *Pupina* (*Kanapa*) *cumingiana* (Pfeiffer) from Tanna Island, New Hebrides that ranged from a notched form to one with no notch, thus forming a transition between *Pupina* and *Kanapa*. The latter name was retained as a convenient sectional name for all the known New Hebridean and the notchless Solomon Island species. The discovery of a notched New Hebridean *Pupina*, described below, raises doubts as to even the sectional utility of *Kanapa*. Just as in the Palau and Caroline Islands there is a series of species showing progressive reduction in the prominence of the apertural notch, so in the New Hebrides there is a transition from the notched new species to the sometimes notched *cumingiana* and notchless *brazieri*. Pending anatomical studies of the species, *Kanapa* has been retained as a convenient term for notchless species, but it certainly is not of generic or subgeneric importance.

Pupina (Kanapa) brazieri (Crosse, 1870)

Pupina (*Kanapa*) *brazieri* (Crosse) : Solem, 1959 : 188.

Remarks. A number of specimens were collected near Luganville, Espiritu Santo by Borys Malkin (CNHM 109428). The shells were relatively larger than those collected by Kuntz (see Solem, loc. cit.) and variation in the largest sample is summarized in Table I. None of the shells showed any sign of an apertural notch.

Pupina (Kanapa) cumingiana (Pfeiffer, 1853)

Pupina (*Kanapa*) *cumingiana* (Pfeiffer) : Solem, 1959 : 189, pl. 9, fig. 8.

A single adult shell collected by J. R. Baker on Vate is 7·0 mm. high, 3·2 mm. in diameter and has a slight trace of an apertural notch.

TABLE I

	Height			Diameter			h/d Ratio				
	Mean	Range	S.D.	Mean	Range	S.D.	Mean	Range	S.D.	Whorls	Range
Partula aurianana Hartman (CNHM 109346) (74 spec.) Mosina Bay, Vanua Lava, Banks Is., New Hebrides	17·174	16·1–18·2	0·499	10·604	9·9–11·8	0·406	1·576	1·47–1·70	0·049	4⅞	
Diplomorpha layardi (Ancey) (CNHM 109474) (72 spec.) trail Karo-Amok, Malekula, New Hebrides. 1000 feet elev. Borys Malkin collector	20·945	18·5–23·4	1·134	14·122	12·7–15·7	0·778	1·484	1·31–1·64	0·083	3⅞	
Diplomorpha peasei (Cox) (CNHM 109475) (75 spec.) Bankaharijitoa above Dunduy, 1500–2000 feet elev., Aoba, New Hebrides. Borys Malkin collector	23·112	20·2–25·2	1·117	17·105	14·8–19·3	0·799	1·352	1·24–1·53	0·053	4⅜+	
Pupina brazieri (Crosse) (CNHM 109428) (18 spec.) Luganville, Espiritu Santo, New Hebrides. Borys Malkin collector, 25th August, 1958	6·450	5·81–8·13	0·334	3·100	2·75–3·25	0·122	2·090	1·98–2·28	0·730		
Pupina malkini Solem (CNHM 109418) (16 spec.) 500–800 feet elev. above Nasaua, Maewo, New Hebrides. Borys Malkin collector, 4th Sept., 1958	5·390	4·94–5·88	0·285	2·680	2·44–2·88	0·182	2·015	1·91–2·14	0·086		
Pupina malkini Solem (British Museum) (8 spec.) Gaua, Banks Group	5·660	5·26–6·00	0·229	2·870	2·63–3·00	0·131	1·980	1·89–2·07	0·058		
Omphalotropis acrostoma Solem (CNHM 109406) (12 spec.) trail Sola-Mosina, Vanua Lava, Banks Group. Borys Malkin collector, 9–11th August, 1958	5·180	4·88–5·75	0·266	3·47	3·25–3·81	0·174	1·490	1·45–1·58	0·039	6+	5¾–6¼
Omphalotropis acrostoma Solem (CNHM 109408) (6 spec.) Vureas, Vanua Lava, Banks Group. Borys Malkin collector, 6th August, 1958	5·100	4·88–5·44	0·184	3·510	3·38–3·75	0·139	1·460	1·39–1·50	0·041	$5\frac{15}{16}$	5⅞–6
Omphalotropis setocincta Ancey ML 40, Brigstock Point, Espiritu Santo, New Hebrides. 11th March, 1944. R. E. Kuntz collector (29 spec.)	4·810	4·47–5·23	0·200	3·220	2·88–3·65	0·160	1·500	1·37–1·59	0·053	5⅜	5–5⅜

Pupina (Pupina) malkini new species

Text-fig. 15

Diagnosis. A species of *Pupina* paralleling the Caroline Island *Pupina brenchleyi* E. A. Smith in the degree of reduction of the apertural notch, but distinguished from all Melanesian and Micronesian species by its skewed apex, shouldered antepenultimate whorl and extremely long penultimate whorl.

Holotype. Chicago Natural History Museum No. 109417, collected at 500–800 feet elevation, above Nasaua, Maewo, New Hebrides by Borys Malkin on 4th September, 1958.

Description. Shell solid, shining, with an orange tint to the basically yellow-horn colouration, surface sculpture absent. Whorls five, sutures of first three slightly indented and whorls a little bit convex. Antepenultimate whorl distinctly shouldered in front at a point well below the middle of the whorl, rounded behind. Penultimate whorl flattened in front, quite elongated, suture not indented and descending

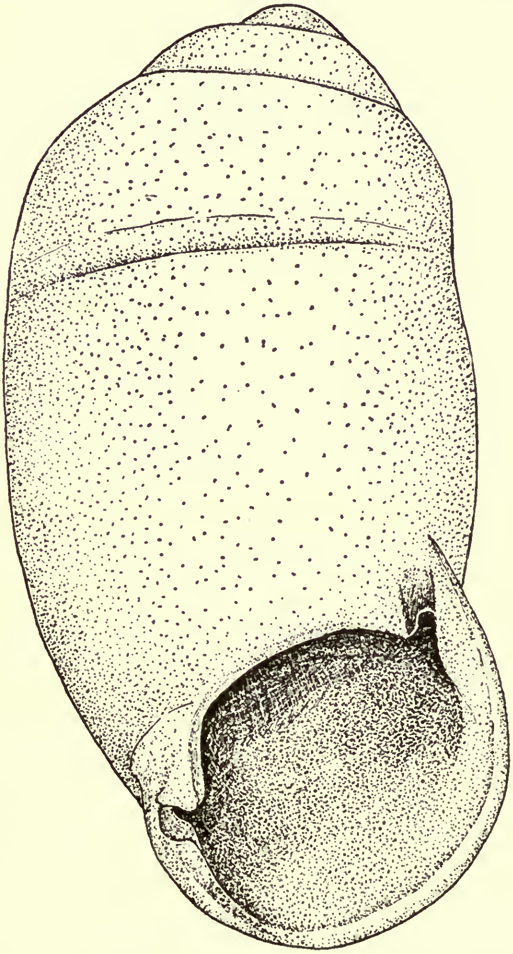


FIG. 15. *Pupina malkini*, new species. Holotype.

rapidly behind. Apex and upper spire usually distinctly tilted to the right. Aperture circular in adults, subovate in juveniles, with a strong diagonal columellar notch (exceptionally widely open in the holotype) and apertural notch composed of a small parietal tooth and a prominent palatal groove that is slightly obscured by a thickening of the lip. Operculum thin, horny, slightly concave multispiral with a central nucleus. Holotype 5·1 mm. high, diameter 2·56 mm., whorls 5.

Paratypes. Chicago Natural History Museum No. 109418, Bernice P. Bishop Museum No. 215240, British Museum (Natural History) No. 1961656 from the type locality.

Range. Vanua Lava, Banks Islands and Maewo, New Hebrides.

Remarks. Size and shape variation are summarized in Table I. Most of the type set corresponds closely to the holotype in form, although some individuals have the apex much less sharply tilted and the penultimate whorl slightly shorter. There is great variation in the shape and degree of openness of the columellar notch. The figured holotype is unusually widely open while most paratypes have a notch that corresponds closely to that of *Pupina keradreni* Vignard (see Clench, 1949 : p. 32, fig. 18–*c*). In three juvenile shells the notch is shallow, nearly vertical and much as in the figures of *Pupinoa* (see Clench, 1949, p. 37, fig. 21), becoming horizontal and partially closed in adults through thickening of the lip. This raises the possibility that the few specimens described as species of *Pupinoa* may be juveniles of species of *Pupina*. The apertural notch is reduced in comparison to that of the Solomon Island *P. keradreni*, but equivalent to the notch of *P. brenchleyi* from the Caroline Islands. In juvenile shells the notch is reduced to the extent found in the Caroline Island *P. complanata* Pease.

On Vanua Lava, Banks Island, Borys Malkin collected one live adult on the trail from Sola to Mosina (CNHM 109419) and four live adults at Vureas (CNHM 109422). In size, shape and apertural characters they fall within the range of variation shown by the type set and no hesitation is felt in referring them to this species.

Pupina brazieri is larger, never has any sign of an apertural notch, lacks the shouldering of the antepenultimate whorl and has a shorter penultimate whorl.

Superfamily RISSOACEA

Family HYDROBIIDAE

Genus *FLUVIOPUPA* Pilsbry, 1911

Fluviopupa brevior (Ancey, 1905)

Fluviopupa brevior (Ancey) : Solem, 1959 : 195–196, pl. 6, fig. 11, pl. 27, figs. 5, 6.

The specimens reported by Baker (1929) from Steaming Hill Lake, Gaua as *Potamopyrgus* sp. were examined and unquestionably are a *Fluviopupa*. Preservation in formalin had seriously weakened and decoloured the shells so that handling was difficult. They are a little more slender and elongated than the Espiritu Santo shells studied previously, but were too delicate to allow the handling needed for accurate measurements or dissection. Possibly the Gaua shells are subspecifically or specifically distinct, but until the extent of interpopulational variation can be determined, taxonomic recognition is not warranted.

Family Assimineidae

Genus ***OMPHALOTROPIS*** Pfeiffer, 1851

Without considerable anatomical studies it will be impossible to adequately classify the species assigned to this genus. Numerous subgeneric and sectional names recognize conchological variations, but none of these names can be considered to recognize phyletic units. A case in point is the meaning of *Stenotropis* and *Oriella*. The former covers elongate, yellowish brown shells with an umbilical keel and no prominent surface sculpture ; the latter species with similar umbilicus and sculpture, but with deeply indented sutures and fewer whorls. Both types are found in the Marianas, Fijis and New Hebrides, and probably the varying forms in each area are more closely related to each other than to their counterpart in the further island groups. The two names are convenient terms to indicate a type of shell structure, but may not represent phylogeny. The endemic New Hebridean group, *Lyrotropis*, is of uncertain affinity to extra-limital forms.

Omphalotropis (Lyrotropis) conella Sykes, 1903

Omphalotropis (*Lyrotropis*) *conella* Sykes : Solem, 1959 : 203, pl. 11, fig. 5.

J. R. Baker found a few juvenile shells on Vate and Borys Malkin collected four nearly adult shells at 500–800 feet above Nasaua, Maewo (CNHM 109403).

Omphalotropis (Lyrotropis) poecila Ancey, 1890

Omphalotropis (*Lyrotropis*) *poecila* Ancey: Solem, 1959: 202–203, pl. 6, figs. 12, 13, pl. 26, figs. 9, 10.

J. R. Baker's collections included specimens from Mt. Touri, Hog Harbour, and East Central Espiritu Santo plus a few from Vate. Borys Malkin found a good set near Luganville and one adult at Nasuli, Baldwin Bay, Espiritu Santo, and a series at 1,500–2,000 feet elevation at Bankaharijitoa above Dunduy, Aoba (CNHM 109367).

Omphalotropis (Stenotropis) acrostoma new species

Text-fig. 16

Diagnosis. A species perhaps most similar to the Caroline Island *Omphalotropis laevis* (Pease), but differing by its less swollen spire, larger umbilicus, thicker lip and more flaring aperture. The New Hebridean *Omphalotropis* (*Oriella*) *setocincta* Ancey is very similar in sculpture and umbilical characters, but has fewer whorls, much more deeply indented sutures and a less flaring aperture.

Type. Chicago Natural History Museum No. 109407, collected on the trail from Sola to Mosina, Vanua, Banks Is., New Hebrides by Borys Malkin on 9th–11th August, 1958.

Description. Shell relatively small, height about 5 mm., elongate conic with the spire not swollen. Surface minutely granulose, dull, without sculpture other than very faint growth lines. Colour a light yellow brown with a dull reddish subsutural zone on the upper whorls and occasionally a reddish tint to the inside of the aperture. Whorls $5\frac{3}{4}$–$6\frac{1}{8}$, sutures only slightly indented and whorls at most moderately convex, never shouldered below the suture. Umbilicus a narrow chink with a moderately conspicuous, white tinted carina. Aperture ovate, moderatelyflaring with thickened columellar lip and heavy parietal callus. Basal lip slightly angulated. Operculum, thin, horny, flexible, with acentral nucleus and a few scattered calcareous granules on the surface. Animal typical of the genus with proboscid cape that is bifurcate dorsally, short stubby grey flecked tentacles; and heavily grey flecked mantle. Sexes separate, but no differences in size of male and female shells. Male with very large cephalic verge situated mid-dorsally. Tip varying from arrow- to axe-shaped. Holotype 5·25 mm. high, diameter 3·5 mm., with 6 whorls.

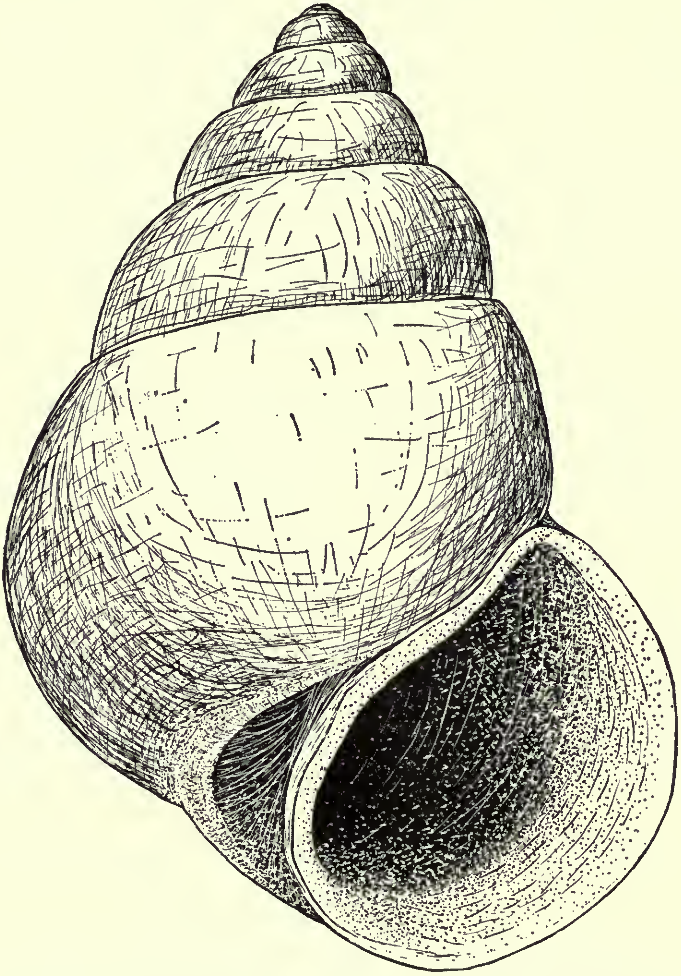


Fig. 16. *Omphalotropis acrostoma*, new species. Holotype.

Paratypes. Chicago Natural History Museum No. 109406, Bernice P. Bishop Museum No. 215241, British Museum (Natural History) No. 1961657 from the type set.

Remarks. The flaring lip, less indented sutures, and one-half more whorl effectively separate *O. acrostoma* from *O. setocincta*. The combination of flaring lip, more whorls and shallower sutures gives the subjective impression that *O. acrostoma* is a much more slender shell with longer spire than is *O. setocincta*. Measurements of the two species show little difference (see Table I) except in whorl count and the apparent difference seems to be an optical illusion.

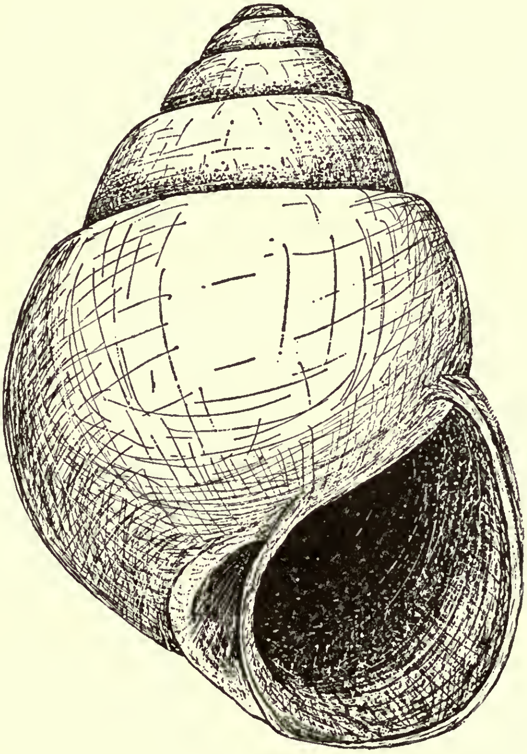


FIG. 17. *Omphalotropis setocincta* Ancey.

Measurements of ten males and ten females did not differ significantly, and, by shell alone, the sex cannot be determined. The gross external anatomy is not distinguishable from that of the Mariana *O. cookei* (Abbott, 1949, p. 265, fig. 1) except for the larger tip on the verge and slightly shorter tentacles. No comprehensive study on the anatomy of *Omphalotropis* has been published. Well preserved examples of the soft parts were available, but time did not permit a study of the internal anatomy.

Besides the type set, four adult males and two females were collected by Borys Malkin at Vureas, Vanua Lava (CNHM 109408).

Omphalotropis (Oriella) setocincta Ancey, 1890

Text-fig. 17

Omphalotropis (*Oriella*) *setocincta* Ancey: Solem, 1959: 200–201, pl. 27, figs. 8, 9.

Remarks. Two dwarf (4·06–4·12 mm. high) adults were collected by Borys Malkin at Norovorovo, Maewo (CNHM 109409). One of these is figured for comparison with the new species described above. J. R. Baker found a few on Vate and four adults on Gaua in 1925. The latter were 3·56–4·37 mm. high, diameter 2·56–2·69, h/d ratio 1·39–1·67 with $5\frac{1}{2}$–$5\frac{5}{8}$ whorls, thus being slightly smaller than Espiritu Santo examples.

C. LIST OF NEW ISLAND RECORDS

The following lists are supplemental to Appendix II in Solem (1959). Only new records or confirmation through specimen examination of listings based on literature records are included. Much of the material reported on above duplicated island records listed in Solem (1959) so that nothing would be gained by presenting a list of all island records mentioned earlier.

Vate

Pupina cumingiana (Pfeiffer)

Malekula

Partula pyramis Hartman
Phrixgnathus glissoni (Ancey)
Orpiella retardata depressa Solem
Dendrotrochus eva eva (Pfeiffer)
Subulina octona (Bruguière)
Opeas pumilum (Pfeiffer)
Diplomorpha layardi Ancey
Pleuropoma sublaevigata (Pfeiffer)
Pleuropoma articulata (Pfeiffer)
Gonatoraphe fornicata (Pfeiffer)

Aoba (=Omba)

Coneuplecta microconus (Mousson)
Dendrotrochus eva eva (Pfeiffer)
Trochomorpha rubens convexa Hartman
Diplomorpha peasei (Cox)
Pleuropoma sublaevigata (Pfeiffer)
Gonatoraphe fornicata (Pfeiffer)
Omphalotropis poecila Ancey

Maewo

Gastrocopta pediculus (Shuttleworth)
Mocella euryomphala Solem
Liardetia samoensis (Mousson)
Dendrotrochus eva eva (Pfeiffer)
Trochomorpha rubens rubens Hartman
Opeas pumilum (Pfeiffer)
Lamellaxis gracilis (Hutton)
Physastra layardi (Ancey)
Pleuropoma sublaevigata (Pfeiffer)
Ceratopoma draytonensis (Pfeiffer)
Gonatoraphe fornicata (Pfeiffer)
Pupina malkini Solem
Omphalotropis conella Sykes
Omphalotropis setocincta Ancey

Espiritu Santo

Phrixgnathus tatariiensis Solem
Pseudosesara tabwemasanana Solem

Gaua

Succinea kuntziana Solem
Mocella euryomphala Solem
Coneuplecta microconus (Mousson)
Trochomorpha bakeri Solem
Lamellaxis gracilis (Hutton)
Ouagapia perryi (Smith)
Physastra layardi (Ancey)
Gyraulus montrouzieri (Gassies)
Pleuropoma sublaevigata (Pfeiffer)
Pleuropoma articulata (Pfeiffer)
Fluviopupa brevior (Ancey)
Omphalotropis setocincta Ancey

Vanua Lava

Partula auraniana Hartman
Liardetia samoensis (Mousson)
Dendrotrochus eva stramineus Sykes
Subulina octona (Bruguière)
Pleuropoma sublaevigata (Pfeiffer)
Pupina malkini Solem
Omphalotropis acrostoma Solem

D. ZOOGEOGRAPHIC COMMENTS

Of the 53 island records listed in section C, seven represent confirmation of early literature records and the remaining forty-six are based on data accumulated during this study. Particularly important are the records from Malekula, Maewo, Omba and Gaua, islands from which none or only a very few non-marine molluscs have been reported. Our knowledge of the fauna is still quite inadequate, since no non-marine molluscs are known from the large islands of Ambrym and Pentecost and very few from the Torres and Santa Cruz groups. Fifty species are now known from Espiritu Santo, 28 from Vate, 21 from Aneiteum (excluding dubious records), 15 from Maewo, and 12 from Tanna, Gaua and Malekula. Undoubtedly these are only partial enumerations of the existing faunas.

Despite our fragmentary knowledge, the data presented above do allow a few general comments about distribution patterns within the New Hebrides. This is in direct contrast with Solem (1959) where the lack of island records forced concentration of effort on generic and family distributions in other island groups. First, there are a number of land snail species that are endemic to the New Hebrides, yet are widely distributed within the island chain without apparent systematically important variations. *Pleuropoma sublaevigata*, reported from twelve islands, is the most widespread endemic, with *Trochomorpha rubens* and *Gonatoraphe fornicata* known from seven islands each, *Dendrotrochus eva eva* and *Succinea kuntziana* from five, *Omphalotropis poecila* probably from four, and *Mocella euryomphala*, *Phrixgnathus glissoni*, and *Omphalotropis conella* from three islands. Both the list of species and the number of island records will undoubtedly be increased by further collecting. These data suggest that there has been probably relatively free faunal interchange between at least certain islands in the not too distant past, or less probably, that the snail fauna is well enough balanced that specific radiation has been comparatively minor in geologically recent times. Regardless of the reason for the wide distribution, the lack of uni-insular endemism is in striking contrast to the faunas of the Marquesas or Hawaiian Islands.

Secondly, we have some data on the degree of faunal relationship between neighbouring islands. Malekula is separated from Espiritu Santo by the narrow and shallow Bougainville Strait, which almost certainly was bridged by land during Pleistocene glaciations. In contrast, Vate Island is separated from Malekula by a wide and very deep water gap. The three islands have several widely distributed endemics (*Pleuropoma sublaevigata*, *P. articulata*, *Gonatoraphe fornicata*, and *Trochomorpha rubens*) in common, and one endemic species (*Phrixgnathus glissoni*) is known only from the three islands. One species (*Phrixgnathus tenuiscriptus*) and one subspecies (*Orpiella retardata depressa*) are restricted to Malekula and Espiritu Santo. Typical *Orpiella retardata* is known from Vate and Aneiteum. Vate and Malekula have *Diplomorpha layardi* and *Dendrotrochus eva eva* in common. *Diplomorpha layardi* is restricted to the two islands and replaced on Espiritu Santo by *D. delautouri*. *Dendrotrochus eva eva* is also found on Epi, Aoba and Maewo, but replaced on Espiritu Santo by the endemic *Dendrotrochus layardi*. Thus, two Espiritu Santo endemics failed to reach nearby Malekula, while two Vate Island forms successfully colonized Malekula. In our present state of knowledge, there is as much faunal resemblance between Malekula and Vate as there is between Malekula and Espiritu Santo.

Finally, the recording of *Trochomorpha bakeri* from Gaua is another indication of the relationship between the Southern and Northern islands (Solem, 1959 : 206) with more distantly related forms in the central group.

The new species described above make no major changes in the general faunal composition of the New Hebridean land snails. Solem (1959 : 316–317) indicated that the New Hebridean endemic land snails contained about equal numbers of Palaeo-Oriental, Southern Relict and Pacific Island taxa. Of the new species recognized above, *Phrixgnathus tatariiensis* is of Southern Relict affinity, *Omphalotropis acrostoma* is Pacific Island, and both *Pupina malkini* and *Pseudosesara tabwemasanana* belong to Palaeo-Oriental groups.

On the basis of information gained during this study and in reviewing the material used in Solem (1959), I would suggest that probably less than half of the New Hebridean non-marine species have been collected and studied at the present time, and that only a small fraction of the data bearing on inter-island distribution is known.

E. REFERENCES CITED

Abbott, R. T. 1949. New syncerid molluscs from the Marianas Islands. *Occ. Pap. B. P. Bishop Museum* **19** (15) : 261–274, 9 figs.

Baker, H. B. 1959. Xanthonychidae (Pulmonata). *Nautilus* **73** (1) : 25–28, 1 fig.

Baker, J. R. 1929. *Man and animals in the New Hebrides.* 200 pp., 43 figs. London.

—— 1935. Espiritu Santo, New Hebrides. *Geographical Journal,* **85** : 209–233, figs., maps.

Clench, W. J. 1949. Cyclophoridae and Pupinidae of Caroline, Fijian, and Samoan Islands. *Bernice P. Bishop Mus. Bull.* **196** : 52 pp., 28 figs.

Pilsbry, H. A. 1948. Land Mollusca of North America (north of Mexico). *Monog. Acad. Nat. Sci. Philadelphia No.* 3, **2** (2) : ix–xlvii, 521–1113, figs. 282–585.

Solem, A. 1959. Systematics and zoogeography of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana, Zoology,* **43** : 359 pp., 18 tables, 38 figs., 34 plates.

—— 1961. New Caledonian land and fresh-water shells. An annotated check list. *Fieldiana, Zoology,* **41** (3) : 415–501, figs. 7–14.

Steenberg, C.-M. 1925. Études sur l'Anatomie et la systématique des maillots (Fam. Pupillidae s. lat.). *Videns. Medd. Dansk naturhist. Foren.* **80** : 211 pp., 34 pls., 50 text-figs.

Verdcourt, B. 1961. Notes on East African Enidae. *Jour. of Conch.* **25** (1) : 9–14.

Wiegmann, F. 1901. Binnen-Mollusken aus Westchina und Central-asien. II. Die Buliminiden. *Ann. Musée Zool. St.-Pétersbourg,* **6** : 220–297, pls. 10–11.

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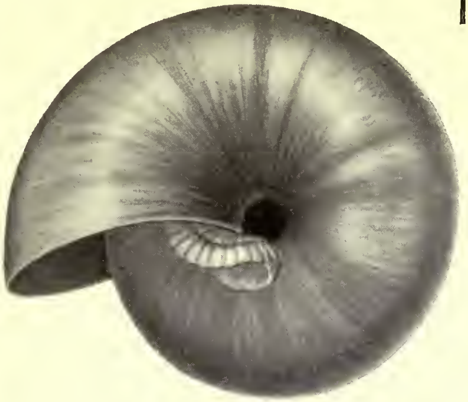
PLATE 1

Figs. 1–3. *Phrixgnathus tatariiensis*, new species.
Figs. 4–6. *Pseudosesara tabwemasanana*, new genus, new species.



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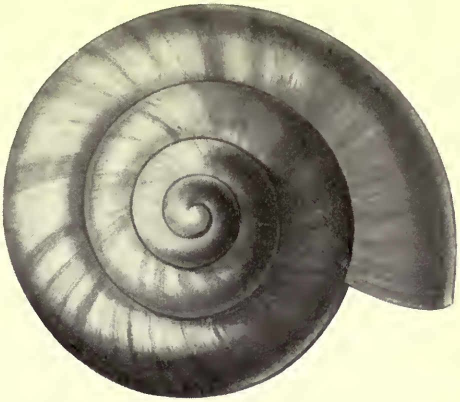

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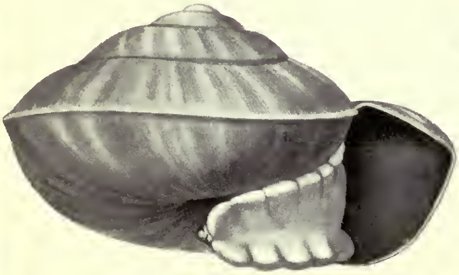

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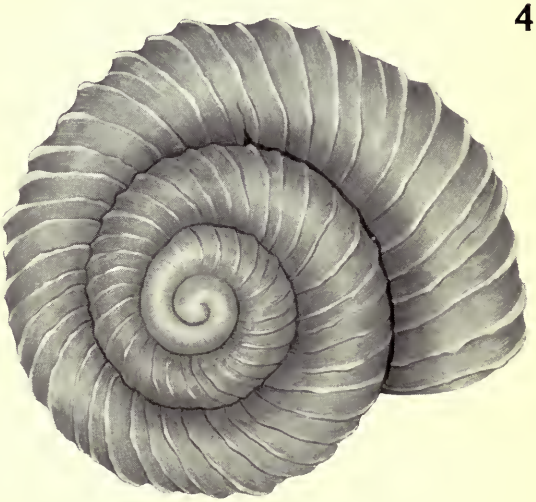

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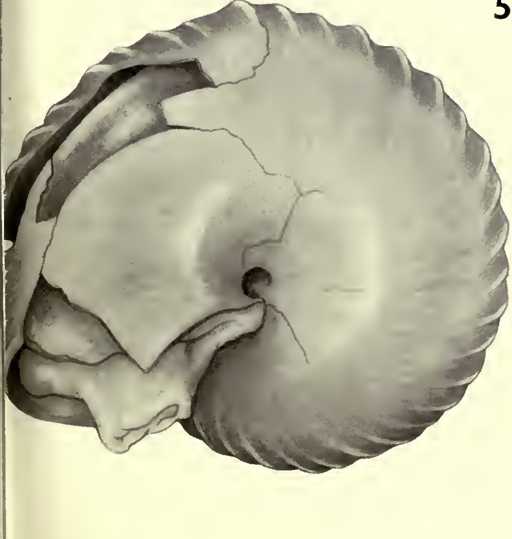

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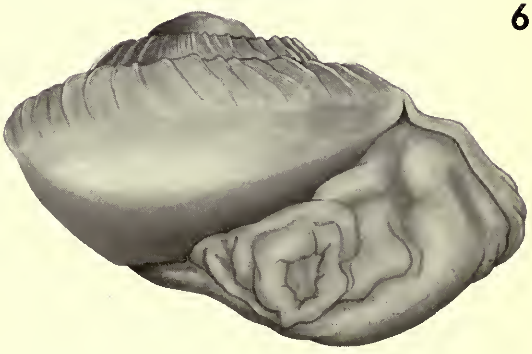

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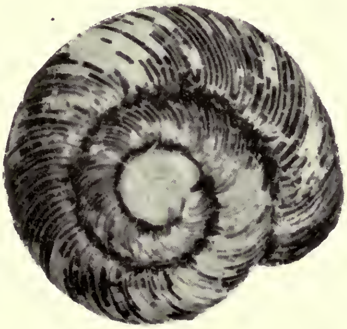
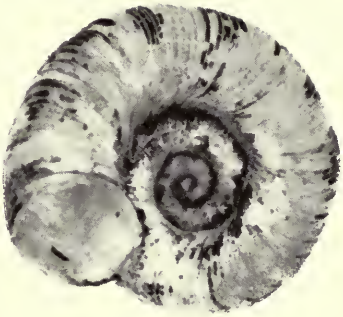
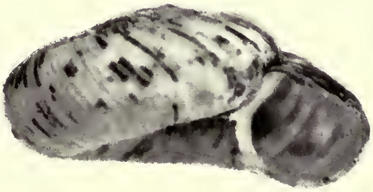
PLATE 2

FIGS. 1–3. *Ouagapia perryi* (Smith). Syntype from Rotuma Island.







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OBSERVATIONS ON THE HETEROMI, AN ORDER OF TELEOST FISHES

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N. B. MARSHALL

BULLETIN OF
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ZOOLOGY Vol. 9 No. 6
LONDON : 1962

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NATURAL HISTORY

BY
N. B. MARSHALL
British Museum (Natural History)

(*Pp.* 249–270; 5 *Text-figures*)

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OBSERVATIONS ON THE HETEROMI, AN ORDER OF TELEOST FISHES

By N. B. MARSHALL

INTRODUCTION

THE order Heteromi was introduced by Gill (1899, pp. 1016–1017) as a sanctuary for fishes of the genus *Notacanthus*. Gill made his decision perfectly plain: " The genus *Notacanthus* has long been shifted from place to place without finding a natural resting-place. It was indeed long ago suggested by Dr. Günther that ' these fishes will, no doubt, have to be placed in a distinct order '; but he has neglected to do so, or to give any reasons why he thought so. The facts now known, however, warrant the isolation suggested, and the order may now be defined by the following characteristics". Such " facts " are out of place here, but it is relevant to consider another order introduced and defined by Gill immediately before the Heteromi. This is the order Lyopomi (Gill, 1899, pp. 1015–1016), proposed to hold the family of halosaurid fishes, another group of deep-sea species ' . . . approximated by most ichthyologists to the Notopterids and Alepocephalids and their supposed allies ".

When revising the Heteromi (as defined by Gill), Goode and Bean (1895) proposed three new genera, *Gigliolia*, *Macdonaldia* and *Lipogenys*. The last was made the generic type of a new family, Lipogenyidae, which had been proposed and defined by Gill (M.S.). The Lipogenyidae are clearly distinct from the Notacanthidae in having a toothless, suctorial mouth and a short-based dorsal fin, composed half of spines and half of rays. It was the last feature that led Boulenger (1904) to the following decision: " The recent discovery of a third family, the Lipogenyidae, which in the structure of the dorsal fin, is exactly intermediate between the two others, has lessened the gap between the Lyomeri (*sic*) (Halosauridae) and Heteromi (Notacanthidae) of Gill, which I have proposed to write in a suborder under the latter name ". Boulenger also regarded the Dercetidae and Fierasferidae as heteromous fishes. Regan (1909, 1910, 1929) followed Boulenger's decision with certain reservations, these being the exclusion of " . . . the Dercetidae, in my opinion probably belonging to the Iniomi, and the Fierasferidae, which are without question specialized Brotulidae " (1909, p. 82). The Heteromi were also given ordinal status.

In his classification of fishes, Berg (1940) has returned to Gill's concept of two separate orders, Halosauriformes (= Lyopomi) and Notacanthiformes (= Heteromi). Berg must have decided that the differences between the two groups were trenchant enough for ordinal status. But the contention of this paper is that the Heteromi (in Regan's sense) form a natural group, the differences between the halosaurs and notacanths not being of a radical nature. In particular, the divergences in fin structure are more apparent than real, for some of the spines of the Notacanthidae are intermediate between fully spinous structures and soft rays. Lastly, study of the swimbladders of both halosaurs and notacanths has revealed close similarities in structural plan. The design of the heteromous swimbladder is also remarkably like that of eels (Apodes), which may well indicate that the two groups diverged from a common ancestor.

SOME DIFFERENCES BETWEEN THE HALOSAURID AND NOTACANTHID FISHES

Consideration of the structural differences between the halosaurs and notacanths, so as to try and see these divergences in better perspective, must obviously precede any attempt to assess the status of the Heteromi. But before this can be done a supposed difference must be eliminated. In defining the order Halosauriformes, Berg, (1940, p. 453), has followed Günther's (1887) description of the anatomy of *Aldrovandia macrochir*, where Günther stated (and showed in Plate LX, fig. 1) that the preoperculum is reduced to a small bone, situated at the lower side of the quadrate. The Notacanthidae have a normal preoperculum and Gill (1889, p. 1015) believed this was also true of the halosaurs. His observations were as follows: " Dr. Günther, in 1868 (*Cat. Fishes*, B.M. vii, 482) assigned to the genus *Halosaurus* a preoperculum produced behind into a long flat process, replacing the sub- and interoperculum. The improbability of such a coalescence of the preoperculum and suboperculum, in view of our knowledge of the genesis and development of these bones, was so extreme that I availed myself of the first opportunity to examine the facts in the case. At Wood's Hole, in 1883, I uncovered the bones sufficiently to detect the true preoperculum, and to recognise that the supposed 'preoperculum' of Günther was the exact homologue of the suboperculum. I deferred publication of any conclusions as to the affinities of the genus, however, till I could examine the skeleton. Meanwhile, a notice and illustration of the skull and scapular arch of the genus have been published by Dr. Günther (*Challenger Deep-Sea Fishes*, pp. 232–236, Pl. 60, figs. 1–8). Dr. Günther at last recognized the true homologues of the opercular apparatus, but has not appreciated the systematic import of the facts disclosed ".

But Gill (perhaps in his eagerness to " have at " Günther) did no more than confuse the issue. Günther's (1868, p. 482) original description of the preoperculum of *Halosaurus* is apt in part: " Preoperculum produced behind into a long flat process, replacing the sub- and interoperculum ". There is no mention of a coalescence between this bone and the suboperculum. The flat process " replaces " the sub- and interoperculum by providing a framework for the gill cover at a place where these two bones are normally found. [In fact the suboperculum and interoperculum are simply concealed by the backward process of the preoperculum (see Text-fig. 1).]

Having appreciated this unusual preopercular development, it is odd that Günther went so astray in his (1887) Challenger Report. Here Gill missed a fine opportunity for Günther did not recognize the " true homologues of the opercular apparatus ". In defining the genus *Halosaurus* (p. 232), Günther described the preoperculum as " rudimentary ", the suboperculum as " large " and the interoperculum as " membranous ". In Plate LX, fig. 2, the " preoperculum " is shown as a small bone immediately below the quadrate, and is described as such by Günther (p. 235). After examining the skeleton of *Aldrovandia macrochir,* from which figures 1–8 of Plate LX were derived, I found that the " preoperculum " is actually the posterior, well ossified part of the quadrate, which must have become detached from the fan-shaped, less robust part of this bone. The complete set of gill cover bones in a specimen of *Aldrovandia affinis* may be seen in Text-fig. 1, which shows the anterior part of the preoperculum in the usual position.

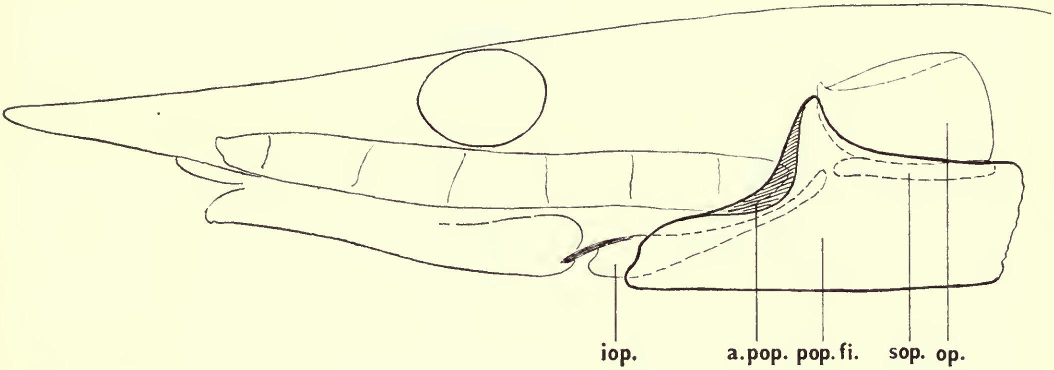


Fig. 1. The head of *Aldrovandia affinis*, showing the gill-cover bones (× 3). The preoperculum has a thickened outline and its anterior part is cross-hatched. A. pop., anterior part of preoperculum ; pop. fl., greatly expanded flange of preoperculum ; iop., interoperculum ; op., operculum ; sop., suboperculum.

Comparison of this figure with Günther's Plate LX, fig. 1, will also show that the bone he labels as the suboperculum is actually the posterior expansion of the preoperculum. This expansion is not a new formation for it carries the (horizontal) continuation of the mandibular lateral line canal, the section that normally turns upwards and curves round the posterior flange of the preoperculum. This flange is generally separated from the more robust anterior part by a ridge, which is also well developed in halosaurids. The extension of the preoperculum is then a greatly expanded posterior flange, a development that is clearly related to the disposition of the sensory canals of the head. In particular, the expansion is keyed to the course of the suborbital canal, which is also unusual. Instead of curving round the orbit, it continues straight backwards and so covers all but a small upper section of the anterior, crescentic part of the preoperculum. The canal tapers to an end on the upper part of the expanded preopercular flange. This being so, there is clearly no room for the (normal) preopercular extension of the mandibular canal, which can only continue straight backwards, and is floored (in the usual manner) by the preopercular flange : hence the great downward extension of this structure, a striking instance of correlation between neuromast disposition and bony development.

All but the neuromasts on the upper parts of the head are thus concentrated below the longitudinal axis of the body, an arrangement that may well have a special significance for the well-being of halosaurs. Observers in bathyscaphes have seen them hovering over the sediments, keeping station against a current by undulations of the after body. Their visual field must certainly be restricted. Perhaps the ventral housing of the highly developed neuromast organs enhances their reception of water disturbances under the body of the fish, both those caused by swimming crustaceans, etc., and those due to the respiratory currents of animals living in the oozes. (Collett (1896) found a small cephalopod (*Rossia*) in the stomach of an *Aldrovandia macrochir*, while Günther (1887) found shrimp-like crustaceans in a Challenger specimen of this species.)

As already stated, the expanded preopercular flange covers the suboperculum and interoperculum. The suboperculum is reduced to a narrow strip of bone and is linked by a ligament to the upper end of the paddle-shaped interoperculum. This bone runs downwards and forwards beneath the preopercular flange and comes into view at the anterior extremity (see Text-fig. 1), where it is joined by a strong ligament to the angle of the lower jaw. Presumably this interopercular-mandibular coupling plays a part, as in other teleosts, in the opening of the jaws.

In brief, all the opercular bones are formed in a halosaur, but the preoperculum is far from rudimentary. The enormous extension of the preopercular flange, which replaces the suboperculum and interoperculum as a covering bone, is related to the unusual disposition of the suborbital and mandibular lateral line canals.

In the Notacanthidae the head canals and gill cover bones follow the usual teleost pattern. These structural contrasts are thus quite striking, but the differences in opercular ossifications are not so trenchant as formerly supposed. A seemingly radical difference concerns the fin rays, which are soft and jointed in the halosaurs, but in both the Notacanthidae and the Lipogenyidae there are some spines in the anal and pelvic fins. The dorsal fin of *Lipogenys* consists of four or five spines followed by five to seven branched rays. Concerning the Notacanthidae, Goode & Bean (1895) described the dorsal fin as consisting of short and free spines and " . . . with soft rays very few or absent ". Regan (1929) also referred to the dorsal spines as " isolated ". But in *Notacanthus* (*sexspinis* and *bonapartei*) and *Macdonaldia* (*challengeri* and *rostrata*), the dorsal spines are not separate entities : Indeed, there is a strong linkage between the radial (basal) supports of the spines (see Text-fig. 2). Each spine also has its own set of muscles. The dorsal spines may thus be regarded as forming the whole or the greater part of a single dorsal fin. (In *Notacanthus* spp. and *Polyacanthonotus* one or two soft rays may be found behind the last dorsal spine.) This being so, there is the following morphological series in dorsal fin structure : Halosauridae (10–13 rays, short-based) ; Lipogenyidae (5 spines + 5 rays, short-based) ; *Notacanthus* (6–12 spines + 1–2 rays, medium—to long-based); *Polyacanthonotus* (29–37 spines + 1 ray, long-based); *Macdonaldia* (27–34 spines, long-based).

This graded series and the finding that the dorsal spines of the notacanths form most or the whole of a single fin, indicates that the two main groups are less distinct in fin pattern than has been supposed. Scrutiny of the structure of notacanth spines strengthens this impression. In *Notacanthus bonapartei*, for instance, the last (2–5) anal spines show definite signs of segmentation (see Text-fig. 3*a*). The divisions between the segmentation are quite clear but they may not reach the surface of the spine. The transition from spines to soft rays is nearly always sharp, each segmented spine being pointed and rigid (in two specimens out of ten the last anal "spine" was somewhat flexible). Indeed, there is no outward evidence (or inward, as far as I could see) of the typical double structure found in a soft ray, the leading surfaces being perfectly rounded and smooth. There may be a median groove down the lower anterior half of the dorsal spines, but whether this is to be regarded as significant is questionable. Most, perhaps all, of the fin spines of notacanths are hollow and do not seem to be so well ossified as those of a typical percomorph.

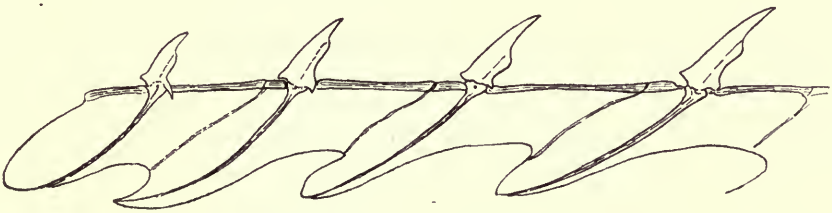
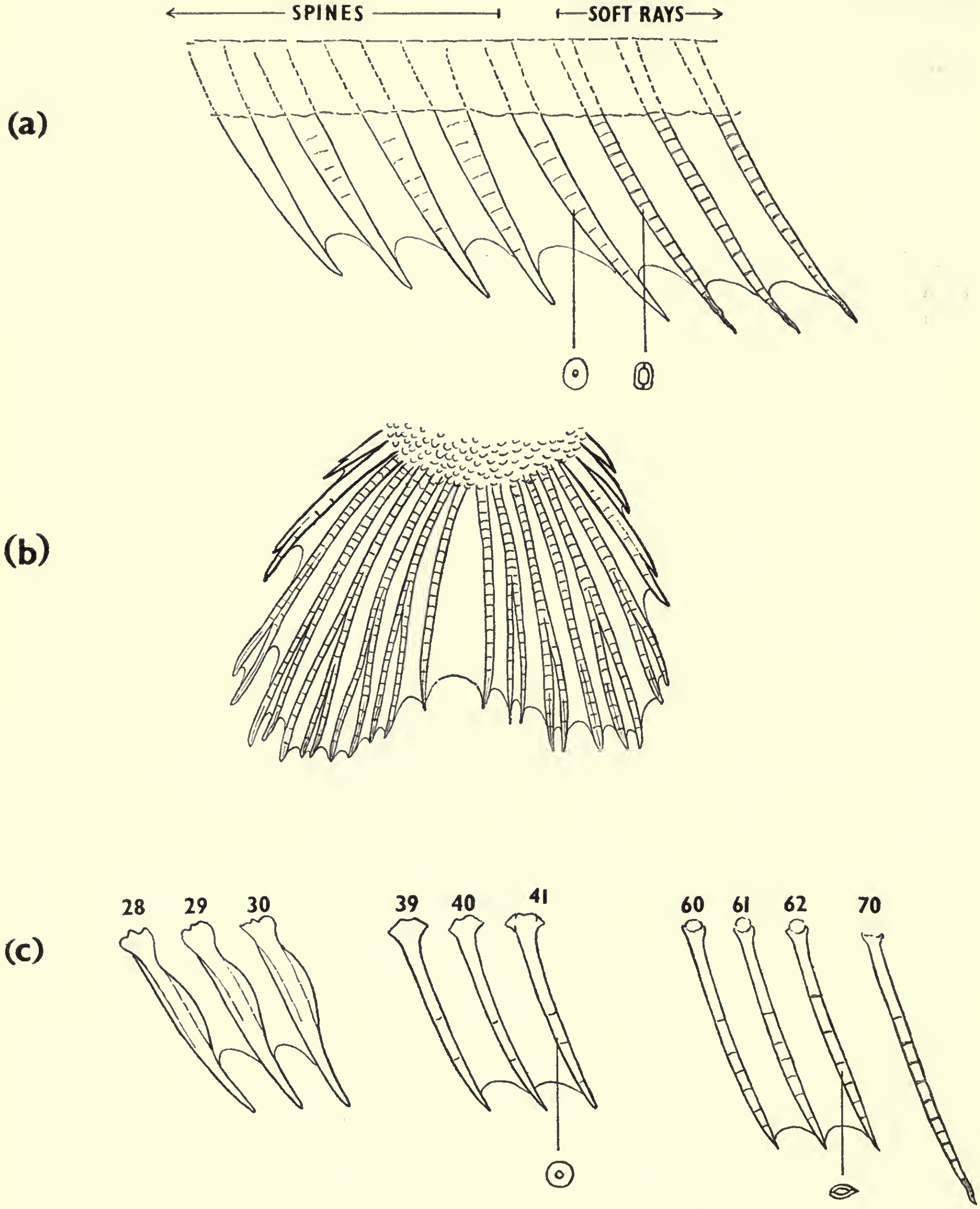


FIG. 2. The first four dorsal spines of *Notacanthus sexspinus*, showing their basal (radial) supporting bones (× 3). The radials fit closely together, but the sutures between them are visible, as shown in the figure.

Each pelvic fin of *N. bonapartei* has three spines and the innermost (and longest) one is usually segmented. This spine may have another resemblance to a soft ray in being forked at the distal end, as may be seen in Text-fig. 3*b*. Out of ten specimens examined, seven had this kind of innermost pelvic spine.

The pelvic fins of *Macdonaldia challengeri* and *M. rostrata* each have a small outer spine, which in the specimen of *rostrata* that I examined had to be dissected out under a binocular microscope. (There are 8 or 9 soft rays.) In the present context it is the structure of the anal fin that is most interesting. The type specimen of *Macdonaldia challengeri* (Vaillant) has 55 anal spines and the last 20 of these are segmented (see Text-fig. 3*c*). The last six of these spines, having one or two extra segments, are somewhat more flexible than the rest, but they still have pointed tips. In a specimen of *Macdonaldia rostrata* the transition between "segmented spines" and rays is less distinct. If the last "segmented spines" are judged to be spinous on account of their rigidity and pointed tips there are 29 anal spines (*sensu lato*). Each of these has a posterior median ridge which contributes


SPINES
SOFT RAYS
(a)
(b)
(c)

to its rigidity. But beyond the last of such spines come several " rays " without this ridge yet still with pointed tips.

If a spine is judged to be a rigid, pointed ray with no trace of segmentation or a double structure, the " jointed spines " of notacanths must be excluded. But are they soft rays ? (To a predator at the pointed end they may deter just as well as " true " spines.) A soft ray is a flexible, jointed structure, made of left and right, closely apposed series of lepidotrichia. If a soft ray is unbranched, the tip is not sharply pointed and rigid. The spines of notacanths with some signs of segmentation lack these features, except that the innermost pelvic spines may sometimes be forked. Rigorous adherence to a spine-soft-ray polarity might mean finding a new name (such as pseudacanths) for the segmented spines of notacanths. If a name must be given, " pseudacanth " would then cover every gradation between a soft ray and a spine. A third category might have some use in taxonomy but the salient feature is the transition from spines to soft rays in the pelvic and anal fins. There can be no better living illustrations of how some spines (*sensu stricto*) may have arisen. (When young notacanths become available, a study of fin development should be illuminating.) In the present context this transition is further evidence that the spiny fins of notacanths are not very different in nature from their homologues in the Halosauridae. [It is also significant that the number of spines in these fins, particularly in the anal fin, may vary considerably within one species (see, for instance, Matsubara, 1938).]

If spinous rays have always had soft-rayed precursors, this transmutation, which involves the suppression of the twin structure, jointing and branching of the lepidotrichia, has occurred several times in the evolution of the teleost fishes. But no one can be sure that spines had no more than this one kind of origin. [Woodward (1942) suggested, for instance, that fin spines might be modified fulcral scales.] Concerning the development of spines, François (1959) has shown that the spinous dorsal rays of *Pterophyllum* arise from a median and *unpaired*, blastematous mesenchyme in the fin fold. Some fin spines might thus have always been spines.

FIG. 3. (*a*) The transition between spiny rays and soft rays in the anal fin of *Notacanthus bonapartei* (× 3). The figure shows 4 spines that bear signs of segmentation, and they follow a plain spine. The last spine is a single structure, not consisting of two halves, as does the first soft ray.

FIG. 3. (*b*) The pelvic fins of *Notacanthus bonapartei* (× 3). The left fin (right in the figure) bears three spines : the right fin has two. The innermost spines are not only partially segmented, but are branched as well.

FIG. 3. (*c*) The transition between spiny rays and soft rays in the anal fin of *Macdonaldia challengeri* (× 5). The numbers above the rays refer to their position in the fin. After robust and ridged spines (like 28, 29 and 30) come partially segmented spines (like 39, 40 and 41), which have a single structure. Following these came rather flexible rays (like 60, 61 and 62) with more segments and a double structure, but with pointed tips. A typical soft ray (70) is shown on the extreme right.

Yet in a classic type of percomorph fish, the striped bass (*Roccus saxatilis*), the third anal spine develops from the first segmented soft ray. Mansuetti (1958) has found that this ray loses its jointed structure, becomes ossified and fuses into a typical spine. He also found that the third anal spine of certain haemulids develops in the same way; while Ginsburg (1953) had already described a similar condition in the scorpion-fish, *Pontinus longispinis*. However, this phenomenon seems to have been first noticed in *Mugil*.

After reviewing the paper by Ryder (1886), Mansuetti gives the following apt summary of present knowledge concerning the development of spinous rays. " Thus he (Ryder) and Goodrich allude to three types of spine formation : (*a*) an outgrowth of a hollow, terminally blind sac of the outside cellular wall of the embryo, exclusive of embryonic ray formation ; (*b*) development from left and right halves of fin rays which fuse together into a hollow rod in the mid-line at an early stage, which is possibly the type of origin of first and second anal rays in the striped bass, and (*c*) development from a well formed soft ray through the processes of structural change and ossification and this, of course, is how the third anal spine formed in the striped bass ". Fin spines may also arise, as already stated, from an unpaired *anlage* in the embryonic fin fold (François, 1959).

But, unlike notacanths, no grown percomorph fish is known to have fin spines that still display some signs of their origin from soft rays. Such tell-tale traces seem to be rare in spiny-finned members of (typically) soft-rayed groups. However, signs of articulation can be discerned in the pungent fin spines of the spiny-rayed (plagopterine) cyprinid fishes (Miller and Hubbs, 1960). Perhaps a careful scrutiny of all manner of spinous rays will reveal other such instances (see Hubbs, 1944). There is also relatively little knowledge concerning the development of spiny rays. When both aspects have been more thoroughly explored a better appreciation should be gained of one of the outstanding events in the history of fishes ; the evolutionary development of spiny-rays. After all, more than half the species of living fishes have fin-spines of some kind or other.

The halosaurs and notacanths are very alike in swimbladder bauplan. As well-preserved specimens of *Notacanthus bonapartei* were available, some description of the swimbladder of this species will first be given. The sac occupies the posterior two-thirds of the body cavity and starts just behind the liver. As Günther (1887) observed, the swimbladder of *Notacanthus* is forked at the front into left and right cornua. The two retia mirabilia originate towards the front of the left fork and they extend backwards within the walls of this structure as far as its junction with the main cavity of the swimbladder. This left-hand fork, as Günther also saw, may have a duct-like forward extension : " A pneumatic duct can be traced for a short distance from the end of the left corner, but is soon lost and does not appear to reach the oesophagus ". But Lozano Cabo (1952) stated that the swimbladder of *Notacanthus bonapartei* was united with the oesophagus by a pneumatic duct. Maul (1955) also found a pneumatic duct in this species, but judging from his drawing this may be the inner lining of the duct. Tucker and Jones (1951) figure a pneumatic duct in a large specimen of *Notacanthus phasganorus*. But in no instance is there any evidence of the duct remaining completely open in an adult fish. Like nearly every species of deep-sea fish with a swimbladder, the Notacanthidae (and Halosauridae) are physoclists. Even if the pneumatic duct opens into the oesophagus, as in the parasitic eel *Simenchelys* (Jacquet, 1920) the swimbladder can function as a closed organ, for the gas gland and retia are very well developed. Apart from this, a *Simenchelys* living near the bottom, perhaps at a depth of several hundred metres, is hardly going to climb to the surface to gulp atmospheric air. On its way down most of its acquired buoyancy would soon be lost.

Returning to the swimbladder of *Notacanthus bonapartei*, the left-hand horn, which will now be regarded as an expanded, posterior part of the pneumatic duct, opens into the main swimbladder cavity at a point about two-fifths of the way down the major axis. Around the opening there appears to be a muscular sphincter. The two retia mirabilia (each about 15 mm. in length in a swimbladder from a 335 mm. fish) end at this point, where the capillaries continue straight towards a corresponding area of gas gland, the cells of which are scattered in rather diffuse, meandering. patches. The retia are thus unipolar. One rete turns back at the above opening and feeds a gas gland in the right-hand fork, which is simply the forward part of the main cavity. The other rete supplies another glandular area in the middle region of the sac (see Text-fig. 4*a*).

The resorbent part of the swimbladder appears to be centred in the expanded part of the pneumatic duct. By-pass branches from the blood vessels forming the two retia extend down the anterior part of the expansion and there are certainly many smaller vessels close to the inner epithelium.

The swimbladder of other notacanthids also has this bauplan. The two retia mirabilia in the posterior pneumatic duct of *Macdonaldia challengeri* (type specimen, standard length 394 mm.) are about 17 mm. long. In a 230 mm. *Notacanthus indicus*, taken by the John Murray Expedition off the South Arabian coast, one rete (length 12 mm.) appears to be considerably wider than the other (see Text-fig. 4*b*). The specimen shows very well the forward continuation of the pneumatic duct, the posterior walls of which contain the two retia. The continuation appears to taper blindly to a point about 10 mm. in front of the origins of the retia. In this specimen I was also able to see that the bulbous part of the pneumatic duct is well supplied with blood vessels, which suggests that this is indeed the resorbent part of the swimbladder.

The bauplan of the halosaur swimbladder is very like that of the notacanths. I have examined three species, *Halosaurus oveni*, *H. parvipennis* and *Aldrovandia affinis*. In *H. oveni* the origin of the two retia mirabilia is a few scale rows behind the base of the pectoral fins and the main sac extends down most of the body cavity. The specimen dissected was 337 mm. in length : the two retia spanned about 20 mm. They are housed in the walls of a posterior, expanded part of the pneumatic duct, which is to the right of the sac, and they end at the (ventral) opening of the duct into the main cavity (see Text-fig. 4*c*). The pneumatic duct continues forward of the retial origins, and it may end, as Günther (1887) found " . . . in a thread attached to the oesophagus ". The retial vein appears to join the hepatic portal system. Each rete supplies a corresponding half of the gas gland. Lastly, there is a short appendix near the front end of the main sac (see Text-fig. 4*c*), which looks

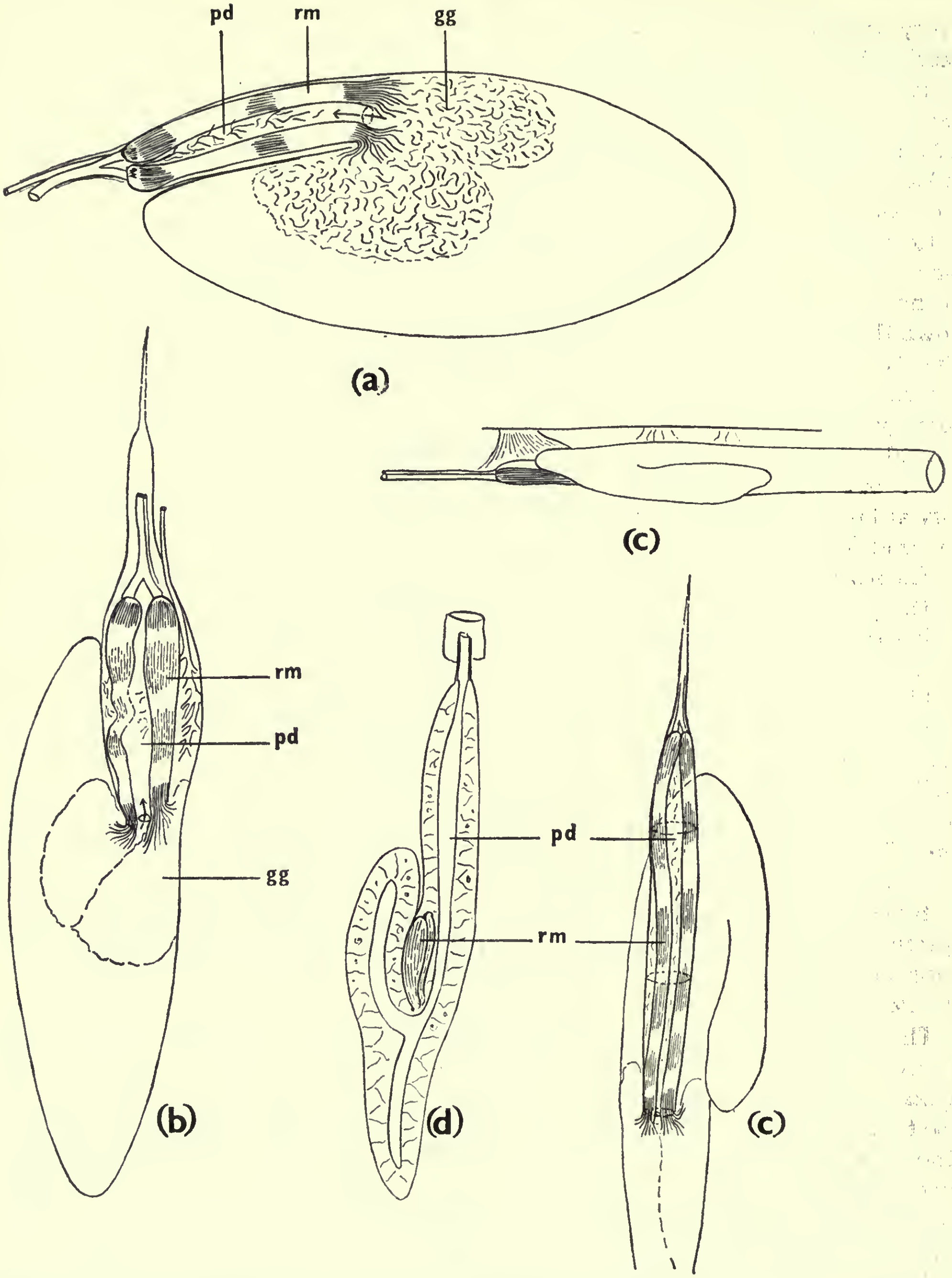


FIG. 4. (*a*) Swimbladder of *Notacanthus bonapartei*, ventral view (× 2); (*b*) Swimbladder of *Notacanthus indicus*, ventral view (× 2.5); (*c*) side view (× 2) and ventral view (× 2.5) of the swimbladder of *Halosaurus oveni*; (*d*) developing swimbladder in an elver of *Anguilla anguilla* (× 12.5). gg., gas gland; rm., rete mirabile; pd., pneumatic duct, the walls of which are highly vascular.

as if it might compensate for any asymmetry in buoyancy due to the off-centre placing of the rete-containing section of the pneumatic duct. But this could only be decided by examining a freshly caught fish with a properly expanded swimbladder.

Except for the absence of this appendix, the structure of the swimbladder in *Halosaurus parvipennis* and *Aldrovandia affinis* is essentially similar to that of *H. oveni*. The lengths of the two retia are about 20 mm. both in an *A. affinis* (length of fish 325 mm.) and a *H. parvipennis* (length 260 mm.).

The design of the swimbladder is thus remarkably similar in the Halosauridae and Notacanthidae. We have also seen that the two groups are basically alike in opercular structure and not very distinct in fin structure. If these facts are considered together with other similarities, such as listed by Regan (1929) and Berg (1940), there is good reason for retaining the order Heteromi in the wide sense. The members of this order would thus be the Halosauridae, the Lipogenyidae and the Notacanthidae. Dr. S. Macdowell, who is preparing a section on the Heteromi for the *Fishes of the Western North Atlantic* has also come to this conclusion, and it is interesting that his views are largely based on a detailed study of the skeletal system. I am most grateful to him for allowing me to see copies of the completed parts of his manuscript.

THE HETEROMI AND THE APODES

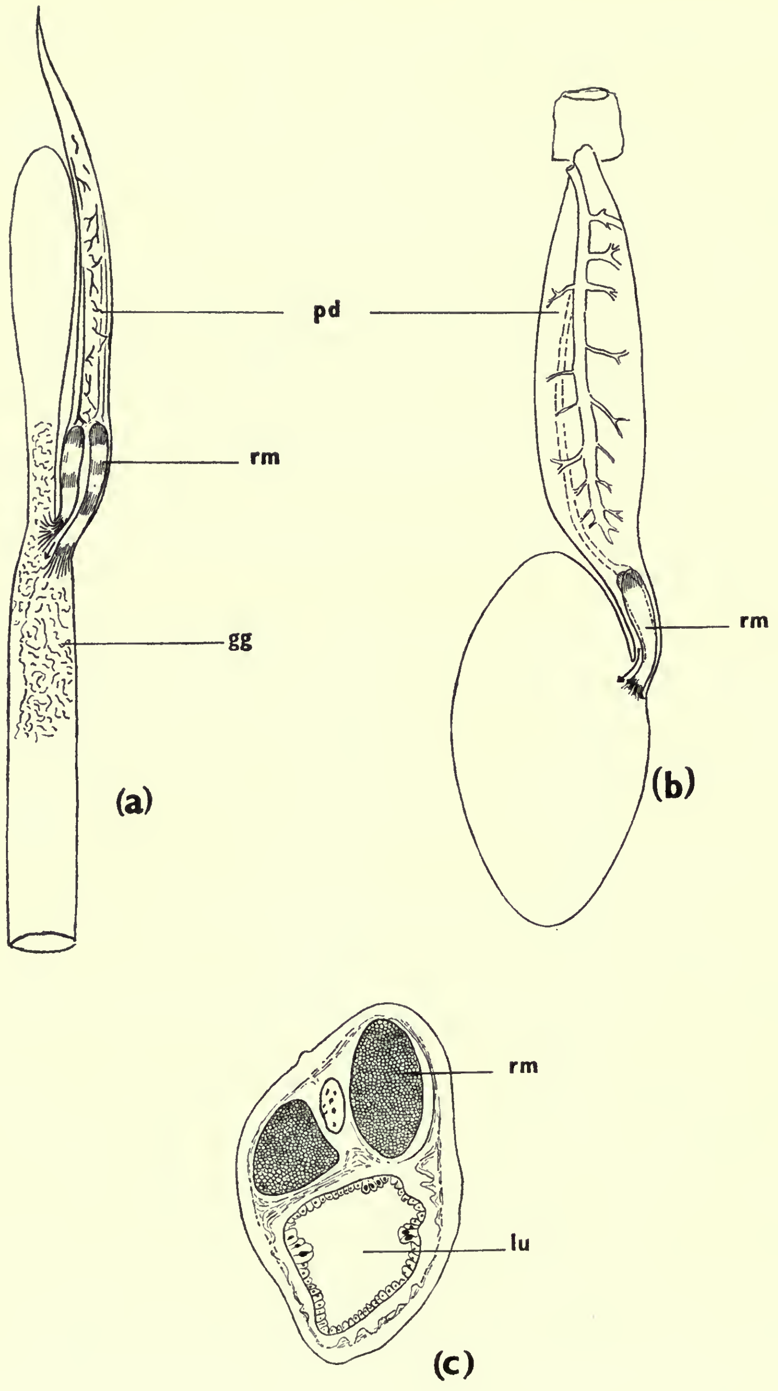
The similar design of halosaur and notacanth swimbladders is not so surprising, but I was less prepared to find that this design is remarkably like that found in eels (Apodes) (see Text-fig. 5). To take the best known instance, the swimbladder of the freshwater eel, *Anguilla* (Woodland, 1911; Fänge, 1953) is like that of a heteromous fish in the following respects:

(i) An expanded, posterior part of the pneumatic duct forms the resorbent part of the swimbladder.
(ii) The walls of the duct contain two retia mirabilia.
(iii) The retia mirabilia end where the duct opens into the main cavity of the swimbladder.

This kind of swimbladder is also found in *Conger conger*, *Myrus vulgaris*, *Ophichthys imberbis* and *O. serpens*, except that the third species appeared to have but one rete mirabile (Woodland, 1911).

Again, *Simenchelys parasiticus* has much the same type of swimbladder, but judging from Jacquet's (1920) figures, the pneumatic duct seems too narrow to form an efficient resorbent surface. Perhaps this is centred in the forward bulbous part of the main cavity, which according to Jacquet is thin-walled.

A forward, somewhat bulbous part of the swimbladder is also found in Synaphobranchus (see Text-fig. 5*a*) and this connects with the main, posterior chamber through a rather narrow neck. Beyond this neck is the opening of the pneumatic duct, which is on the left side of the posterior chamber. The more expanded, posterior part of the duct contains two retia mirabilia, each about 10 mm. in length. The pneumatic duct continues forward well beyond the origin of the retia and finally seems to taper to a thread, which is attached to the roof of the body cavity just


pd
rm
gg
(a)
rm
(b)
rm
lu
(c)

below the kidneys. (This attachment is just ahead of the extremity of the bulbous section.) The resorptive part of the swimbladder appears to be confined to the widened, posterior part of the pneumatic duct. Well forward of the origin of the retia, the walls of the duct contain many blood vessels.

The only notable difference between swimbladder structure in the Heteromi and Apodes is that the latter have bipolar retia mirabilia, whereas the retia of the halsaurs and notacanths are unipolar (see Marshall, 1960 for further discussion of these two retial types). But the retia of *Synaphobranchus* are unipolar and the same may be true of *Simenchelys*, judging from Jacquet's (1920) figures. Bipolar retia are clearly not an invariable feature of eel swimbladders.

The swimbladders of the Apodes and Heteromi thus conform to a strikingly similar bauplan, which suggests that the two groups might have evolved from a common ancestor. As we see them today, both types of fishes are decidedly specialized, but certain other likenesses might be expected if they really had a common origin.[1] Relevant similarities in form would seem to be as follows :

(1) Both orders consist of elongated, long-tailed fishes with a spine composed of many vertebrae (with parapophyses not fused to the centra).
(2) Upper intermuscular bones (epineurals) and pleural (lower) ribs are developed (some eels also have epipleural (upper) ribs).
(3) The scales are cycloid (although most eels are scaleless).
(4) There is a long, many-rayed anal fin (reduced in certain eels) and the pelvic fins are abdominal [in eels pelvic fins are only known in the fossil genus *Anguillavus*, which had eight-rayed pelvic fins. (*c.f.* 8–10 rays in the Heteromi)].
(5) Head features. The eyes are covered by " spectacles " formed from the skin of the head. The upper jaw is bordered by the premaxillae and maxillae (in eels the premaxillae coalesce with the mesethmoid and sometimes with the vomer : in the Notacanthidae only a small backward part of each maxilla is included in the gape). There is also a marked resemblance between the form and arrangement of the frontals and parietals, the latter meeting in the middle line of the skull. There is then no contact between the frontals and the supraoccipital.
(6) There are no oviducts.

Discussion of the differences between the heteromous fishes and the eels would be largely concerned with their specializations. In eels these are : the highly modified respiratory and opercular systems (entailing the separation of the pectoral girdles from the skull and the loss of the post-temporal bones); the loss of scales and the pelvic fins; the firmly built skull, including the fusion of the premaxillae to the ethmoid region; the modified suspension and variable development of the palatopterygoid bones, etc. (see Gosline, 1959 for an interesting discussion of eel specializations in relation to the habits of these fishes).

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[1] Do heteromous fishes have a leptocephalus larva ?

FIG. 5. (*a*) anterior part of swimbladder of *Synaphobranchus kaupi*, ventral view (× 2.5) ; (*b*) ventral view of swimbladder of *Anguilla anguilla* (× 2) ; (*c*) a transverse section through the pneumatic duct of *Anguilla*, showing the two *retia mirabilia* in the walls. The epithelial lining of the lumen is shown (after Woodland, 1911). gg., gas gland ; lu., lumen of pneumatic duct ; rm., rete mirabile ; pd., pneumatic duct, with highly vascular walls.

The more obvious features of the Heteromi are: (1) the projection of the snout beyond the mouth; (2) the development of a forward, "rostral" extension of the ethmoid region; (3) the spine-like process of the maxilla; (4) the absence of a tail fin; and (5) various skeletal reductions, e.g. the absence of the mesocoracoid, postcleithrum, orbitosphenoid and basisphenoid.

Returning to the similarities between the two orders, the eye "spectacles" could be convergent features, necessary protections for the eyes of rooting and burrowing fishes. (The firm build of the fore part of the skull in eels and the rostral extension of the heteromous fishes are also likely to be adaptations for burrowing.) But even disregarding this probable optical convergence, the eels and Heteromi still have numerous common features, underlying, as it were, their more obvious specializations. Undoubtedly the most marked resemblance is in swimbladder bauplan. If one knew that this was no more than an instance of convergence, the other similar characters would not readily lead one to suppose the two orders could have had a common origin. But there is such a close and detailed resemblance in swimbladder structure (see pp. 261–262), and, moreover, this bauplan is unique to these two orders.

To continue this line of thought, it will be relevant to look at some of the uses that can be made of swimbladder structure in the major classification of teleosts. The Isospondyli are a good starting point, and not simply because this order includes some of the most primitive species.

Considering first the Clupeoidea, and beginning with *Chirocentrus*, Ridewood (1905) regarded it as a clupeoid fish. Indeed, he concluded thus: "*Chirocentrus* agrees so closely in the structure of its skull with the Clupeidae, that appeal must be made to other organs of the body for evidence to support the views of those who would make of it a distinct family, the Chirocentridae . . . ". Berg (1940), however, separates *Chirocentrus*, even making it the basis of a new suborder of Isospondyli (and quotes Jacobshagen to the effect that teleosts have no spiral valve in the intestine, such as *Chirocentrus* is said to possess). But *Chirocentrus* has a swimbladder that is very like that of a clupeid. Each tubular extension to the (appropriate) inner ear ends in two vesicles that are lodged in prootic and pterotic bullae: the pneumatic duct opens into the stomach (Ridewood, 1905; Srivastava, 1956). Moreover, in *Chirocentrus* elongated branches of the lateral line canals run over the surface of the gill cover bones; a character that is thus not uniquely clupeid. Indeed, Clausen's (1959) description of the head canals in *Denticeps* reminds one of the clupeid branching system. After remarking that the detailed pattern of ramifications is unique among teleosts, Clausen does state that there is some similarity to the condition found in *Clupea*. In view of this it is interesting to find that the pneumatic duct enters the stomach and that swimbladder diverticula are present in the ears as in the clupeids.

The clupeids and *Chirocentrus* are thus quite closely related, and in two striking respects, bauplan of swimbladder and lateral line system, they are more than suspiciously like *Denticeps*. There may even be good reason for putting the Denticipitidae, the Chirocentridae, and the Clupeidae in a division Clupeiformes[1] of the suborder Clupeoidea. As already implied, the characters of the division could reside in the stethoscopic type of swimbladder (with an opening into the stomach) and in the fine system of lateral line branches over the gill cover bones. Moreover, the clupeids and *Denticeps* (but not *Chirocentrus*) have scutes along the mid-ventral line of the trunk, while in Chirocentrus and the clupeids there is little or no extension of the lateral line canals over the trunk.

If this be admitted, it would then be sensible to group the Elopidae and Albulidae in the Elopiformes and the Alepocephalidae and Searsidae in the Alepocephaliformes. The elopiform fishes have, *inter alia* ; a leptocephalus larva ; numerous branchiostegal rays (except in *Pterothrissus*) ; parietals meeting before the supraoccipital ; a subtemporal fossa, and pelvic fins with 9 to 15 rays. [*Elops* and *Megalops* have a large gular plate and there is a rudiment of this bone in *Albula.*]

It is less easy to define the Alepocephaliformes, but there can be little doubt of the relationship of the two families. They lack a swimbladder and generally have small pectoral fins that are placed low down on the shoulders. Photophores are present or absent and there is a tendency for the loss of scales on the head. The dorsal fin nearly always arises behind the mid-standard length, either overlapping the anal fin or being opposed to it. Nearly all alepocephalids and searsids have 7–9 branchiostegal rays.

Turning to the Stomiatoidea, one gets a decided impression that they form a natural group, but it is by no means easy to find diagnostic features. However, a good many species have retained a swimbladder, and, as I have said elsewhere (Marshall, 1960), this has a unique kind of bauplan : it is paraphysoclistous with a single, bipolar rete mirabile at the posterior end.

The deep-sea salmonoids also have a characteristic kind of (euphysoclistous) swimbladder containing numerous micro-retia. Again, study of this organ reinforces the idea that these fishes belong to a natural group, which I suggested might be the Argentiniformes (Marshall, 1960). The other salmonoids (Salmoniformes) have an open swimbladder with a short pneumatic duct at or close to the anterior end of the sac. One species (*Coregonus lavaretus*) is known to have micro-retia (see Fahlen, 1959), but these seem to be absent in *Salmo*. (Close study of a range of salmonid swimbladders would be particularly interesting.)

Thinking of this tendency in salmonoids to develop a diffuse retial system, it is interesting that *Esox* also has micro-retia (see Corning, 1888). One is reminded of Berg's (1940) contention that the esocoid fishes originated from osmeroid fishes at the end of the Cretaceous period. Perhaps this parallelism in an unusual kind of retial structure adds point to Berg's idea. At all events, and ranging further afield, it might well be worthwhile to make a survey of swimbladder structure in the " salmonoid " fishes of the Southern Hemisphere (Galaxiidae, Retropinnidae and Haplochitonidae). On the one hand, they seem to have certain affinities to the esocoid fishes, and, on the other, to the northern salmonoids (see Gosline, 1960). Cursory examination of the swimbladder of *Retropinna retropinna, Haplochiton zebra* and *Galaxias attenuatus* certainly shows that the position and gross features of the pneumatic duct are similar to those in salmonids and esocoids. But *Retropinna* has a two-chambered swimbladder, and in the other two species the pneumatic duct opens into the stomach. Closer study is obviously needed.

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[1] The use of the ending " -formes " is surely more appropriate to a division than to an order. Clupeiformes is too specific a name for an order. To take but a few instances, *Opisthoproctus*, *Macristium*, *Phractolaemus*, *Cromeria* and *Gymnarchus* hardly impress one as being " clupeiform ".

The mormyroid and notopteroid fishes also have a distinctive swimbladder. In the former each ear is closely coupled to a vesicle derived during development from a bifurcating, forward extension of the sac. Yet this is one of many diagnostic features of a remarkable group of isospondylous fishes. Concerning the notopterids, Dehadrai (1957) has resolved certain ambiguities in the early work of Bridge (1889) on *Notopterus borneensis* and studied other species. Each anterior caecum of the swimbladder is associated with the anterior part of the sacculus (not with the utriculus, as formerly supposed). Apart from this, there are several other distinctive features of the notopterid swimbladder, such as the sub-spherical sac and the ventral diverticula.

Now according to Berg (1940), the Hiodontidae are notopteroid fishes, but the differences between this family and the Notopteridae seem more impressive than their similarities. After discussing the skeletal features of both groups, Ridewood (1904) concluded that : " Although in *Notopterus* and *Hyodon* there are vesicles of the swimbladder on the lateral face of the otic region of the cranium, it does not necessarily follow that these structures have had a common origin. The connection between the swimbladder and the ear must not be relied upon too implicitly as indicating close relationship between such fishes as possess it ". But a more significant point is that reliance can only be given to structures that are closely similar in all essential respects. [The Clupeiformes (*sensu stricto*) may be taken as a paradigm of this contention.] Indeed, Ridewood (1904) found that each otic connection in *Hiodon* is made by a " great vesicle of the swimbladder ". The complete description suggests that the *Hiodon* type of auditory coupling is not *closely* like that of a notopterid. In fact, the divergence seems substantial. But once more, what is needed is a careful anatomical study of the swimbladder in *Hiodon*. We might then come nearer to appreciating the systematic position of this interesting genus of fishes.

The Ostariophysi also contain some primitive teleosts. But the order is readily distinguished from the Isospondyli by the two chains of ossicles (Weberian apparatus) linking the ears with the anterior chamber of the swimbladder. The structure of these extra auditory channels are remarkably and closely similar in the characoid and cyprinoid fishes. The Siluroidea might well be regarded as a separate order if it were not for the Weberian apparatus etc. But in all essentials of an intricate mechanism, the siluroids are like the other Ostariophysi. As Chranilov (1929) shewed, there are no trenchant differences between the Weberian apparatus of the cyprinoids and siluroids. One divergence concerns the greater degree of fusion of the anterior vertebrae in siluroids : others involve such structures as the ossa suspensoria of the swimbladder and the details of linkage between the sinus impar, claustrum and stapes (see Chranilov, 1927, 1929). But the most reasonable conclusion is that this whole elaborate mechanism, particularly the sequence of ossicles and the remarkable modification of the labyrinths, is very unlikely to have been independently acquired by the siluroids.

Turning to the Iniomi, swimbladder structure fully reveals the Myctophidae as a natural group, distinct from the Neoscopelidae and unlikely to have had a stomiatoid ancestry (Marshall, 1960). The Miripinnati also have a unique kind of swimbladder (Bertelsen and Marshall, 1956).

To end, but not complete, this review of swimbladder structure and its uses, both actual and potential, in the classification of teleosts, we may consider the position of the Thoracostei (sticklebacks). That these fishes seem to be most closely related to the Solenichthyes is suggested by certain structural congruences (see Berg, 1940), and the difficulty in placing the genus *Indostomus*. While the armature of the body reminds one of a syngnathid, Bolin (1936) has shown that it is more like the sticklebacks in a number of characters. Whether this genus should be put in its own order or in a suborder of Thoracostei can only be determined by a more detailed study of its anatomy. Regarding the relationship between the Thoracostei and Solenichthyes, it may be significant that both have a euphysoclistous, two-chambered swimbladder. The forward chamber contains one or more retia mirabilia and a gas gland, while the rear chamber is concerned with the resorption of gases. But two chambered swimbladders of this basic type have been evolved independently in a number of distantly related groups of teleosts. Yet again we must turn to the details of structure if we are to make the best use of what is now a possible structural clue to relationships.

Returning to one main purpose of this paper, we have seen that the detailed bauplan of the swimbladder in Heteromi and Apodes gives more than a hint that these two orders may well have had a common ancestor, one that evolved from an isospondylous kind of teleost. Without such structural evidence, this conclusion would not easily come to mind.

A final thought concerns our reactions to skeletons. We are impressed by their solid appearance, their architectonic forms, and their seeming wealth of characters. But soft parts may often be more conservative than hard parts, preserving a basic bauplan that can be put to good use in classification. Bone, after all is related to blood, and next to blood is the most plastic tissue in the vertebrate body. This appreciation, which I owe to Professor A. J. E. Cave, is something to keep in mind. Bone is largely shaped by the form and functional needs of the soft organs. It is, so to say, the servant and not the master of these structures.

SUMMARY

Regan (1909) and other authorities considered the order Heteromi to consist of the halosaurs and notacanths, but Berg (1940), following Gill (1889), placed them in two separate orders: Halosauriformes (= Lyopomi) (Halosauridae) and Notacanthiformes (= Heteromi) (Lipogenyidae and Notacanthidae). The main characters distinguishing the two orders are the development of fin spines in the notacanths

(absent in halosaurs), and the (supposed) unusual structure of the gill cover bones in the halosaurs.

While the preoperculum is normally formed in the notacanths, the corresponding bone of the halosaurs is believed to be rudimentary. But Günther's (1887) paper is midleading, the bone called the preoperculum actually being the posterior part of the quadrate. The true preoperculum is well developed, but it is remarkable in bearing a very accentuated flange, which covers the small suboperculum and a club-shaped interoperculum. The flange is extended so as to carry the posterior part of the suborbital lateral line canal, which continues straight backwards instead of curving round the orbit. There is thus no room for the (normal) preopercular continuation of the mandibular canal, the course of which is parallel to the suborbital canal.

In fin pattern and spine formation the Lipogenyidae are intermediates of the Halosauridae and Notacanthidae. There is, in fact, a morphological series in these features (Halosauridae→Lipogenyidae→*Notacanthus*→*Polyacanthonotus*→*Macdonaldia*). Moreover, the dorsal spines of notacanths are not isolated elements, but are parts of a single fin, one with a well-knit framework of basal supporting bones. Careful scrutiny of the fin spines of notacanths also shows that some of the spines (certain of the pelvic spines and the most posterior anal spines) still display signs of segmentation : they have spinous and soft-rayed features. The inner pelvic spines may even be branched in the manner of a soft ray.

This hardly seems to show that the differences between the halosaurs and notacanths are trenchant enough to justify ordinal status for these two groups. Study of the design of their swimbladders reinforces this conclusion. In both groups the swimbladder has a main chamber into which opens a large pneumatic duct, which in adult fishes may taper off to a connection (but not an open one) with the oesophagus. The walls of the expanded, posterior part of the pneumatic duct contain two large, unipolar retia mirabilia, which enter the gas gland at the opening of the duct into the main cavity. The expanded part of the duct is highly vascular and must serve for the resorption of gases. In short, the congruence between the swimbladders of halosaurs and notacanths is very close, which fact, combined with their other resemblances, gives ample indication that they form a natural group and a single order Heteromi.

The design of the heteromous swimbladder is very like that found in eels (Apodes), a design that is unique among bony fishes. Indeed, the resemblances are detailed enough to suggest that the Heteromi and Apodes evolved from a common ancestor, which must have been an isospondylous kind of teleost. While the fishes of both orders are highly specialized, there are a number of (other) common features to support this conclusion, which must, however, be largely based on the bauplan of the swimbladder.

The concluding part of the paper is given to a review of the uses, both actual and potential, of swimbladder structure in classifying the teleosts. A striking instance, but only one among many, concerns the common development of a stethoscopic type of swimbladder in the Chirocentridae, Clupeidae and Denticipitidae. This unique kind of auditory linkage and certain other unusual common features, particularly the extension of lateral line canals over the gill cover bones, could suggest that these three families form a natural group (Clupeiformes) of the clupeoid fishes. Consideration of this and other such instances suggests that soft parts may often be more conservative than hard parts, preserving a basic bauplan that can be useful in systems of classification. Bone, after all, is the servant rather than the master of the soft organs of vertebrates.

REFERENCES

Berg, L. S. 1940. Classification of fishes both recent and fossil. *Trav. Inst. zool. Acad. Sci., U.R.S.S.*, **5** : 87–512. English Translation. Ann Arbor, Michigan, 1947.

Bertelsen, E. & Marshall, N. B. 1956. The Miripinati, a new order of teleost fishes. *Dana Rep.*, no. 42, pp. 1–34.

Bolin, R. L. 1936. The systematic position of *Indostomus paradoxus* Prashad and Mukerji, a freshwater fish from Burma. *J. Wash. Acad. Sci.*, **26** : 420–423.

Boulenger, G. A. 1904. Fishes (Teleostii) : in *The Cambridge Natural History*, Vol. VII, pp. 541–727.

Bridge, T. W. 1889. The air bladder and its connection with the auditory organ in *Notopterus borneensis*. *J. Linn. Soc. Lond.* (*Zool.*), **27** : 503–540.

Chranilov, N. S. 1927. Beiträge zur Kenntnis des Weber'schen Apparates der Ostariophysi. I. Vergleichend-anatomische Ubersicht der Knochen-elemente des Weber'schen Apparates bei Cypriniformes . *Zool. Jb. Nata.*, **49** : 501–597.

—— 1929. Beiträge zur Kenntnis des Weber'schen Apparates der Ostariophysi. 2. Der Weber'sche Apparat bei Siluroidea. *Zool. Jb. Anat.*, **51** : 323–462.

Clausen, H. S. 1959. Depticipitidae, a new family of primitive isospondylous teleosts from West African freshwater. *Vidensk. Medd. fra Dansk Naturh. Fore.*, **121** : 141–151.

Collett, R. 1896. Poissons provenant des campagnes du Yacht ' l'Hirondelle ' (1885–1888). *Result. Camp. sci. Monaco*, **10**, pp. 198.

Corning, H. K. 1888. Beiträge zur Kenntnis des Wundernetzbildungen in den Schwimmblasen der Teleostier. *Morph. JB.*, **14** : 1–53.

Dehadrai, P. V. 1957. On the swimbladder and its relation with the internal ear in genus *Notopterus* (Lacépède). *J. zool. Soc. India*, **9** : 50–61.

Fahlen, G. 1959. Rete mirabile in the gas bladder of *Coregonus lavaretus*. *Nature*, **184** : 1001–2.

Fänge, R. 1953. The mechanisms of gas transport in the euphysoclist swimbladder. *Acta physiol. Scand.* **30** (Suppl. 110) : 1–133.

François, Y. 1959. La nageoire dorsale—anatomie compareé et evolution. *Ann. Biol. Paris*, (3) **35** : 81–113.

Gill, T. 1889. The halosauroid fishes typical of a special order. *Amer. Nat.* **23** : 1015–1016.

—— 1889. The Notacanthid fishes as representatives of a peculiar order. *Ibid.* **23** : 1016–1017.

Ginsburg, I. 1953. Western Atlantic scorpion-fishes. *Smithson. misc. Coll.* **121** (8) : 1–103.

Goode, G. B. & Bean, T. H. 1895. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. No. XXIX. A revision of the order Heteromi, deep-sea fishes, with a description of the new generic types *Macdonaldia* and *Lipogenys*. *Proc. U.S. Nat. Mus.* **17** : 455–470.

Gosline, W. A. 1959. Mode of life, functional morphology, and the classification of modern teleostean fishes. *Syst. Zool.* **8** (3) : 160–164.

—— 1960. Contributions toward a classification of modern isospondylous fishes. *Bull. Brit. Mus. nat. Hist. Zool.* **6** : 327–365.

Günther, A. C. 1868. Catalogue of the fishes in the British Museum, **7**, pp. 512.

—— 1887. Report on the deep-sea fishes collected by H.M.S. Challenger during the years 1873–1876. *Rep. Sci. Res. Challenger Zool.* **22** : 1–335.

Hubbs, C. L. 1944. Fin structure and relationships of the phallostethid fishes. *Copeia* (2) : 69–79.

Jacquet, M. 1920. Contribution à l'anatomie du *Simenchelys parasiticus* Gill. *Result. Camp. sci. Monaco*, **56**, pp. 76.

Lozano Cabo, F. 1952. Estudio preliminar sobre la biometria, la biologia y la anatomia general de *Notacanthus bonapartei* Risso. *Bol. Inst. esp. Oceanogr.* **49** : 1–30.

Mansuetti, R. 1958. The development of anal spines and soft rays in young striped bass, *Roccus saxatilis* Contr. No. 113. *Chesapeake Biol. Lab.*, pp. 1–12.

Marshall, N. B. 1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. *Discovery Rep.* **31** : 1–122.

Matsubara, K. 1938. Studies on the deep-sea fishes of Japan X. On a new fish *Notacanthus fascidens*, belonging to Heteromi, with special reference to its variation. *Bull. Jap. Soc. Sci. Fish. Tokyo*, **7** : 131–136.

Maul, G. E. 1955. Monografia dos peixes do Museu Municipal do Funchal. Ordem Heteromi. *Biol. Mus. Funchal*, **8**, Art. 20 : 5–19.

Miller, R. R. & Hubbs, C. L. 1960. The Spiny-rayed cyprinid fishes (Plagopterini) of the Colorado River System. *Misc. Publ. Mus. Zool. Univ. Mich.* No. 115, pp. 39.

Regan, C. T. 1909. The classification of teleostean fishes. *Ann. Mag. nat. Hist.* **3** : 75–86.

—— 1910. Notes on the classification of the teleostean fishes. *Seventh Int. Zool. Congress Boston, Cambridge, Mass.* pp. 16.

—— 1929. Article on fishes. Fourteenth Edition of the *Encyclopaedia Britannica*, London and New York.

Ridewood, W. G. 1904. On the cranial osteology of the fishes of the families Mormyridae, Notopteridae and Hyodontidae. *J. Linn. Soc. Lond. Zool.* **29** : 188–217.

—— 1905. On the cranial osteology of the clupeoid fishes. *Proc. zool. Soc. Lond.* **2** : 448–493.

Ryder, J. A. 1886. On the origin of heterocercy and the evolution of the fins and fin-rays of fishes. *Rep. U.S. Comm. Fish* (1884) : 1018–1026.

Srivastava, P. N. 1956. On the air-bladder of *Chirocentrus dorab* (Forsk.), and the relationship of family Chirocentridae with Clupeidae. *Zool. Anz.* **156** : 284–288.

Tucker, D. W. & Jones, J. W. 1951. On a rare deep-sea fish *Notacanthus phasganorus* Goode (Heteromi-Notacanthidae) from the Arctic Bear Isle fishing grounds. *Bull. Brit. Mus. nat. Hist. Zool.* **1** : 67–79.

Woodland, W. N. F. 1911. On the structure and function of the gas glands and retia mirabilia associated with the gas bladder of some teleostean fishes, with notes on the teleost pancreas. *Proc. zool. Soc. Lond.* pp. 183–248.

Woodward, A. S. 1942. The beginning of the teleostean fishes. *Ann. Mag. nat. Hist. Ser.* 11, **9** : 902–912.

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BY
J. P. HARDING
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Pp. 271–296; Plates 1–10; 1 Text-figure

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DARWIN'S TYPE SPECIMENS OF VARIETIES OF *BALANUS AMPHITRITE*

By J. P. HARDING

DARWIN (1854), p. 197, and again on p. 242 vividly describes the great variability of *Balanus amphitrite* and *B. tintinnabulum* and the difficulty he had in coming to the decision as to whether the various varieties he established for these two species should be regarded as varieties or as separate species. *Balanus amphitrite* like *B. tintinnabulum* is frequently found attached to ships and much of the extreme tendency to vary may well, as Darwin himself suggested, be due to their frequently being transported to new localities. Since Darwin's time, many workers have been faced with the same problem and are hampered by the fact that Darwin was unable to publish many illustrations and that his descriptions of the animal parts of the varieties are inadequate by present standards more than a century later. It is now forty-five years since Pilsbry (1916, pp. 93–94) wrote, " The definition of the sub-species of *Balanus amphitrite* is a very intricate problem . . . first of all the Darwin collection must be restudied and type localities for his varieties selected ". The purpose of this paper is to publish the results of such a study. Much of the material studied by Darwin no longer exists ; but there is a cabinet of dry shells mounted on slabs in the British Museum. In the account which follows these specimens are referred to the slab to which they were attached, e.g. Slab 17.1.22. There are also a number of microscopic slides of mouth-parts and other appendages dissected by Darwin now in the University Museum of Zoology, Cambridge ; these are referred to by reference numbers used in the catalogue at Cambridge and written on the slide, e.g. Cambridge Slide 151. In addition Darwin prepared a series of dry specimens of the various varieties of *Balanus amphitrite* for the British Museum and for many years these have been on public exhibition mounted on slabs with two lists of the specimens in Darwin's handwriting alongside ; one list is of " Shells " and the other of " Opercular Valves ", and these will be referred to by the number used in Darwin's lists, e.g. Shell 28, Opercular Valve 4. It was anticipated that the most useful material for the present purposes would be on these slabs but they have proved disappointing. The lists correspond with the specimens only approximately, a number of specimens are now missing and others have evidently been substituted at some time by other material.

Darwin describes nine varieties or sub-species of *Balanus amphitrite* and for most of these I have been able to find and select as lectotype, a specimen complete with opercular valves and animal parts which it has been possible to dissect although it has been dry for over 100 years. The mouth-parts and other appendages have been mounted on a microscope slide and descriptions and figures of these and of the parts of the shell of the same specimen, taking each variety in turn, form the basis of this paper.

The dried and shrivelled animal parts of some of the barnacles were restored with 1% solution of trisodium phosphate but usually it was found to be sufficient merely to introduce a dilute solution of potassium hydroxide into the shell of the barnacles and leave it for twenty-four hours. The animal parts were then washed out of the shell with distilled water and transferred to lactic acid in which they were dissected. Bubbles of carbon dioxide formed by the interaction of the lactic acid with carbonates helped to inflate the shrivelled parts and could then easily be removed by placing the specimen on a glass slide, covering it with a small piece of thin polythene and stroking this from above with a blunt needle under a stereoscopic microscope. The mouth-parts and various appendages as they were dissected away were mounted in order on a glass slide in polyvinyl lactophenol with lignin pink. Studies of the internal structure of the shell were made from as similar a specimen as possible to the lectotype, the method used being essentially that described by Read (Read, 1960), though sheets of " wet or dry " carborundum paper were used for the grinding and ordinary metal polish for the polishing.

Balanus amphitrite amphitrite Darwin

Balanus amphitrite Darwin, 1854, p. 240.
Balanus amphitrite var. *communis* Darwin, 1854, p. 240, pl. 5, figs. 2*e*, *h*, *l*.
Not *Balanus communis* (Pulteney), 1799, p. 25.
Balanus amphitrite var. *denticulata* Broch, 1917, p. 133, text-fig. 14.

Lectotype. (Plate 1, *a–g*, Pl. 2, *a–k*.) A complete specimen chosen from about forty others on a piece of bamboo on which the name *Balanus amphitrite* is clearly written in Darwin's writing. Registered No. B.M. 40.9.15.17. Locality Natal, Dr. Krauss. The shell has been left on the bamboo and re-registered—Reg. No. B.M. 1961.12.6.1c, but the opercular valves have been mounted separately (B.M. 1961.12.6.1a). The animal parts have been dissected and mounted on a microscopic slide (B.M. 1961.12.6.1b).

Paralectotypes

(1) The remaining barnacles on the bamboo, excluding those which are small and pink in colour which are *B. venustus*, B.M. 1961.12.6.1f (see below)

(2) Similar specimens on a second shorter piece of bamboo which is probably but not certainly part of the same material, B.M. 1961.12.6.3c.

(3) Shells 28 and 29, without opercular valves, listed as " var. *communis* ; ship from West Indies ". B.M. 1961.12.6.6c–7c.

(4) Shells 1, 2, 6 and 7. Listed as " var. *communis* ; ship's bottoms ". All without opercular valves. Locality unknown. B.M. 1961.12.6.8e–11e.

(5) Opercular Valves 4, listed as " var. *communis* (Natal) ". One scutum and one tergum. These are very similar to those of the lectotype and are probably from the same material. B.M. 1961.12.6.12e.

(6) Opercular valves listed as " var. *communis* " ; No. 6, B.M. 1961.12.6.13e. One scutum from Faro ; No. 7, B.M. 1961.12.6.14e. One scutum and one tergum

from "Philippine Arch". No. 11, B.M. 1961.12.6.15e, one scutum and one tergum from Smyrna; No. 15, specimen now missing, from Sydney; No. 2, B.M. 1961.12.6.16e, three scuta and three terga from an unknown locality; No. 3, B.M. 1961.12.6.17e, one scutum and one tergum listed as "pale sub. var." from an unknown locality.

(7) A row of six terga on a slab separate from those in the cabinet labelled *B. amphitrite* of which the first, No. 6, has "var. *communis*" written under it in what may be Darwin's writing. There is no locality for these specimens. B.M. 1961.12.6.18e.

(8) Slab 17.1.7, one complete shell without valves or animal parts and six separated varieties. Labelled by Darwin "*Balanus amphitrite*". B.M. 1961.12.6.22e.

(9) Slab 17.1.10, two large specimens on oyster shells and one or two smaller ones labelled *Balanus amphitrite* by Darwin. B.M. 1961.12.6.23e.

NOTE. Shells now in positions 31 and 34 must have been substituted for the original specimens here as they are both *niveus* and not "*communis*" as they should be, according to Darwin's list.

Pilsbry (1916, p. 55) notes that it was Darwin's habit to give the name *communis* to the typical form of any species that had a number of varieties. The modern procedure however, is to give the type variety or sub-species the same name as the species and in this case what Darwin calls *Balanus amphitrite* var. *communis* should be *Balanus amphitrite* var. *amphitrite*, or if the form is treated as a sub-species as I propose to do, simply *Balanus amphitrite amphitrite*. The name *communis* is in any case inadmissible as it is preoccupied by *Lepas communis* Pulteney which is a synonym of a different species of *Balanus*—*B. perforatus*.

Darwin did not select a holotype, so that it falls to me to select a lectotype to serve its purpose. It would have been satisfactory to have selected one of the specimens that had been listed by Darwin as "var. *communis*", however, none of these is complete, either the opercular valves are missing or valves are all that remain. None of these specimens have any of the animal parts and very few of them are from known localities. Darwin, p. 246, writes that he has seen specimens of the typical form "var. *communis* from Natal associated with var. *venustus*". The specimens on the bamboo are from Natal, most of them are of the "communis" form while others are of the *venustus* form. There is a large number of complete specimens and Darwin has written *Balanus amphitrite* on the bamboo itself. I, therefore, select one of the *communis*-like specimens on the bamboo to be the lectotype of *Balanus amphitrite* Darwin and, therefore, of *Balanus amphitrite amphitrite*. This is the specimen photographed (Pl. 1, *a–b*). The opercular valves have now been separated and cleaned and the animal parts dissected and the labrum, mandibles, maxillae and both of each of the six pairs of cirri have been mounted in order on a slide and photographs of a selection are given on Pl. 2. A second specimen from the other piece of bamboo was also dissected for comparison and study but has not been figured—I could find no essential differences. The figure of the section of the shell-wall (Pl. 1, *h*) is from a separate, incomplete specimen taken from the first piece of bamboo (B.M. 1961.12.6.4d).

DESCRIPTION

Size. The shell of the lectotype (Pl. 1, *a*, *b*) has a greatest diameter of 12·8 mm. and a height measured along the slope of the larger lateral of 12·2 mm. and along the lateral of the opposite side of 5·5 mm., the barnacle having grown much more on one side than the other. The greatest diameter of another specimen on the main piece of bamboo is 17·7 mm. and a specimen on the second piece has the greatest basal diameter of 22 mm. The largest specimen in the collection is one of those on Slab 10 with a basal diameter of 30·2 mm.

Colour. The shells of the specimens on the pieces of bamboo including the lectotype have an off-white ground colour with longitudinal dark slate coloured stripes with a slightly violet tinge, a colour which is very similar to that of Darwin's coloured figure, Pl. 5, *2e*. The number of stripes and their thickness is variable. Those of the lectotype can be seen in the photographs. Most of the shells on the bamboo have stripes which are considerably broader than the white interspaces. There is often a white stripe of extra breadth in the middle of a compartment or at its edges. The stripes are narrower than the interspaces on shells 1, 2, 6 and 7 and the colour of the stripes of shells 2 and 6 is more violet especially towards the base of the shell. The radii are whitish, often with flecks of colour, see below.

Shape. The specimens on the bamboo including the lectotype and also " shell 28 " from the West Indies are all very similar in shape to one another and have the profile to the rostrum convex and that of the carina concave. Shells 1, 6, 7 and 29 are of a low conical form with straight profile to the rostrum and are more like Darwin's figure in shape than is the lectotype.

Parietes. Pl. 1, *h*, is a photograph of a polished section of one of the parietes. The pattern of the interlaminate figures can be seen without difficulty but is most easily described with the aid of the diagrammatic representation given in Text-fig. 1. This shows a portion of shell-wall sectioned parallel to the base and polished to show the pattern of the interlaminate figures. The pores are large and evenly spaced. The septa (s) between them extend inwards as vertical ribs (r) which may themselves have flutings (f). The portions (d) of the outer lamina which come opposite the pores are dark purplish in colour and more translucent than the rest of the shell. Individual pores, however, such as that marked (p) often situated near the middle of a compartment do not have this dark portion of the outer lamina opposite them. Such a pore may be recognized from the outside by the presence of an exceptionally broad white stripe (w) such as mentioned above under the description of the colour. Running down the sagittal plane of the septum is a nuance, or difference in structure, which is more opaquely white than the rest of the shell substance and in section shows as a white line (a) running down the middle of each septum from the internal rib almost to the outer lamina where it becomes broken up into irregular patches. In the inner lamina, tree-like patterns (b) are produced by off-shoots of opaque white nuances from this line. Each of the internal ribs of the shell-wall contains a part of this tree-like pattern and it can be seen that the fluting of the ribs corresponds with the white branches of the " top of the tree ". The radii are broad and whitish in colour but in the lectotype and some other specimens they are freckled with specks of colour similar to that of the stripes of the shell. These flecks of colour are in the septa themselves and not in the material which fills the interspaces. They are slightly below the outer surface. The septa have denticuli on their lower sides which are sometimes conspicuous when the sutural edge of the radius is examined but are often blunt, few in number and difficult to see.

The radii of the lectotype and the others on the bamboo and those of the two specimens on Slab 10 have summits more or less parallel to the base while the radii of specimens 1, 2, 6, 7, 28 and 29 have more oblique summits.

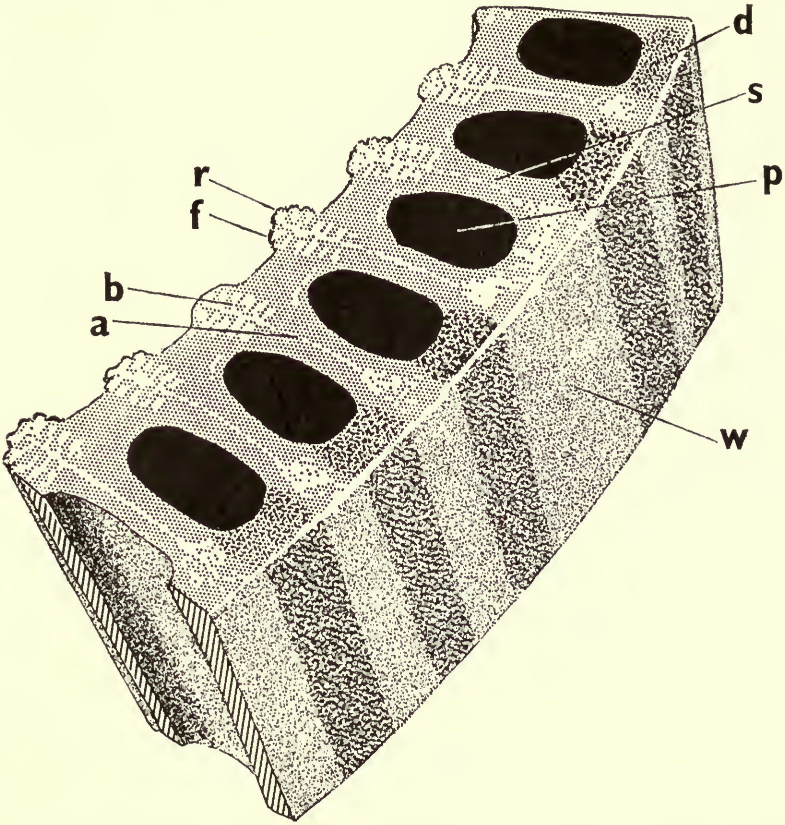

FIG. 1. Piece of parietal wall of *Balanus amphitrite* s. str. sectioned parallel to the basis and polished showing the patterns visible when lit by glancing illumination. Diagrammatic.

(*a*) white line running down septum ; (*b*) " tree-like " pattern ; (*d*) section of coloured shell stripe ; (*f*) fluting to internal rib ; (*p*) pore ; (*r*) rib ; (*s*) septum ; (*w*) extra-wide white stripe. For further explanation see text.

The scutum of the lectotype is shown in Pl. 1, *c–d*. The outer surface is rather smooth with the growth lines visible but not very prominent. The articular ridge is prominent and about half the length of the tergal margin. The adductor ridge is straight and parallel to the occludent margin. The pit for the lateral depressor muscle is very shallow. The internal surface is roughened especially in the apical half of the valve. The other scuta identified by Darwin as belonging to " var. *communis* " and listed above are all rather similar although some of them have more prominent growth ridges. The scuta and terga of most specimens, including the lectotype are white on the inside.

The tergum of the lectotype (Pl. 1, *e*, *f*) agrees very closely with Darwin's description of that of " the commonest purple-stripe forms " which is detailed and rather long and need not be repeated here (Darwin, 1854, p. 244). Most of the specimens labelled " var. *communis* " by Darwin have a similar short, broad spur and only one or two of them have a narrow spur like that of his figure 2(1).

The labrum of the lectotype (Pl. 2, *a*) has twelve or thirteen teeth on each side which continue down into the notch where they gradually become smaller and disappear.

The mandible and maxilla are shown in (Pl. 2, *j*, *k*) and call for no special comment, the maxilla has eight to nine smaller spines between the two pairs of large spines.

The cirri shown in (Pl. 2, *b–g*) agree very well with the description given for his var. *denticulata* by Broch (1927, p. 135) including the curved spines on the inner and outer faces of the basal segments of the 3rd cirrus. These are shown in an enlarged photograph in Pl. 2, *h*.

I have placed the var. *denticulata* Broch in the synonymy of *amphitrite* s. str. as such essentials as the teeth on the maxilla and the structure of the 3rd cirrus strongly support this. The shape of the shell described by Broch (1927) is like that of Darwin's figure (Darwin, 1854, pl. 5, 2, *e*) and like some of the paralectotypes especially shells 1, 2 and 7, these all having concave profiles to the rostral plate. The shape of the shells of the lectotype and paralectotypes on the bamboo is rather different as the rostral plates of these have convex profiles. It is possible that this is a growth response to the curved shape of the bamboo.

Balanus pallidus pallidus Darwin

Balanus amphitrite var. *pallidus* Darwin, 1854, p. 240, pl. 5, figs. *2c–k*.
Balanus amphitrite var. *candidus* Darwin in M.S.

Lectotype. (Pl. 3, *a–d*) a selected specimen from Slab 17.1.25, B.M. 1961.12.6.36c, this has been dissected and the valves, B.M. 1961.12.6.36a, and the animal parts, B.M. 1961.12.6.36b, are now on slides. Locality unknown.

Paralectotypes

(1) Slab 17.1.25. Several other barnacles remaining on the slab after the lectotype was removed. B.M. 1961.12.6.43c, e, most of them are complete with opercular valves and animal parts. One of them, B.M. 1926.12.6.43d, has been ground to give a section of parietal wall. Locality unknown.

(2) Shell 3. A shell complete with opercular valves but no animal parts. This is the specimen of Darwin's figure (Darwin, 1854, pl. 5, *2d*), B.M. 1961.12.6.37c. Locality unknown.

(3) Shell 4. A very similar, slightly shorter shell with no valves or animal parts. Locality unknown. B.M. 1961.12.6.38c.

(4) Shell 5. A group of three small shells complete with opercular valves and probably with animal parts. Darwin's manuscript list reads, " on wood W. Indies Brit. Mus.". The specimens are no longer on wood. Two intact specimens B.M. 1961.12.6.39c, one shell with valves B.M. 1961.12.6.39c, animal parts of same B.M. 1961.12.6.39b.

(5) Shell 11. This is a large specimen with a conical shell complete with opercular valves supported on cotton wool but no animal parts. The shell has been deformed presumably by the toxic effect of the copper sheathing of the hull to which it was attached in the way described by Stubbings (1959). This is listed by Darwin as " var. *candidus* from West Coast of Africa ". B.M. 1961.12.6.41c.

(6) Shell 13. A well formed conical shell without valves or animal parts on a portion of a much larger shell of *Balanus tintinnabulum* listed by Darwin as " var. *candidus* on *B. tintinnabulum* on ship's bottom ". B.M. 1961.12.6.42c.

(7) Slab 17.1.26. Two shells attached to one another, one empty and one with opercular valves and probably animal parts. Two scuta and two terga are also mounted on this slab and there are positions where other shells and valves have been attached but are now lost.

(8) Slab 17.1.27. B.M. 1961.12.6.45e. With one complete shell, three pieces of separate parietes, four scuta, five terga and three positions now empty, the pieces having been lost.

(9) Slab 17.1.34. B.M. 1961.12.6.46e. A group of about 10 specimens on the walls of a *Balanus tintinnabulum*, four of these specimens are complete. Mounted on the slab alongside are three scuta and two terga and there is a space for another piece which is now missing. One has provided a section of parietal wall. B.M. 1961.12.6.46d. (Pl. 3, *m*.)

(10) Slab 17.1.37. B.M. 1961.12.6.47e. This contains a piece of wood which no longer has any barnacles on it. Five other specimens which were once attached to the slab are now also missing. There remains one very obliquely grown specimen which is complete, three scuta, one tergum and two minute specimens on a bivalve shell.

(11) Opercular Valves 1. Two scuta and four terga listed by Darwin as " var. *pallidus* ". B.M. 1961.12.6.48e.

The name *pallidus* occurs only once in Darwin's handwriting. This is the entry for this variety in his list of " opercular valves ". In every other case in his list of shells Darwin uses the name *candidus*, that is for shells no. 3, 4, 11, 13. The slabs listed above are also all named " var. *candidus* " in Darwin's handwriting on the back of the slab, written either in pencil or in ink. The name *candidus* is clearly the manuscript synonym of *pallidus*. The specimens agree with Darwin's diagnosis of the variety and one of them, as noted above, is his figured specimen.

Description. The height of the lectotype is 13·8 mm. and its greatest diameter is 8·2 mm. The largest specimens are two on Slab 17.1.25, one with a height of 13·8 mm. and diameter of 13·8 mm. at the base and 12·8 mm. at the top and the other with a height of 13·2 mm., and greatest diameters at the base and top respectively of 13·4 and 11·7 mm. This and nearly all the specimens are of the cylindrical form. Apart from very young specimens the only ones with conical shells are Shell 9 (the distorted specimen), Shell 13, and one of the ten specimens on Slab 17.1.34. Shell 9 has a basal diameter of 17·6 mm. in one direction and 14·4 mm. at right angles to this, and the diameter at the top is 9 mm. × 7 mm., and the height 10·8 mm.

Shell 13 is a conical specimen with a base of 15·3 × 13·1 mm. and aperture of 8·3 × 4·6 mm. and a height of about 9 mm. The one with a conical shape of the ten specimens on Slab 17.1.34 is very similar to the last but is smaller. All the others on this slab are of the cylindrical type.

The shell is white in colour with sometimes a thin purple line along the edges of the parietes. A photograph of the polished section of parietal wall is given in Pl. 3, *m*. It seems to be characteristic of this species to have, in addition to the normal row of large pores, subsidiary smaller pores outside them. There is the usual white line between the major pores and this branches distally to give subsidiary white lines between the subsidiary pores. Between each major pore and the inner face of the wall there is, in section, a white line parallel to the plane of the wall and about the length of the width of the pore; the "tree-like" pattern is sometimes more distinct than in the specimen photographed but it is often more obscure.

The scuta often have a triangular blue-black area both internally and externally as can be seen in Pl. 3, *g* and *h*.

The radii are usually oblique and have inconspicuous striations parallel to the base, the septa being opaquely white and the material between them hyaline white. The denticuli of the septa on the sutural edge of the radius are very inconspicuous.

The scuta on Pl. 3, figs. *g* and *h* are typical with the articular ridge about half the length of the occludent margin. There is a faint ridge running between the articular ridge and the basal margin which fades out at both ends and reaches neither the articular ridge nor the basal margin.

The pit for the depressor muscle is so shallow as to be almost non-existent. Externally the growth ridges are distinct; the apical part of the scutum is roughened on the inside.

The tergum, Pl. 3, *e*, *f*, has a long and narrow spur about its own width distant from the basi-scutal angle. I do not believe the tergum figured by Darwin (1854, pl. 5, 2*k*) is of this species.

The crests for the lateral depressor muscle are well developed and project beyond the basal margin. In addition to the growth lines the external surface shows some longitudinal striations which correspond with the crests for the lateral depressor muscle on the other side of the valve.

The labrum of the dissected specimen, Pl. 3, *j*, has two teeth on each side.

The maxilla, Pl. 3, *l*, has two upper and two lower spines much longer than the others.

The cirri are shown in Pl. 3, *n*–*q*. The 3rd cirrus has short broad segments and is very hairy, Pl. 4, *r*.

Balanus pallidus stutsburi Darwin

Balanus amphitrite var. *stutsburi* Darwin, 1854, p. 240.

Lectotype. (Plate 4, *a–f*; Pl. 5, *a*, *c*, *e–k*), the only complete specimen remaining of those studied by Darwin, one of four specimens on Slab 17.1.12. On the back of the slab in Darwin's writing is " *Balanus amp.*". All four specimens are very similar to Shell 8 which is listed by him as " var. *stutsburi* ". The lectotype had written on the shell in ink the old register number 41.1.3.34, which has made it possible to trace the locality from which it came, which Darwin may not have known. It was among material from the West Indies presented by J. E. Gray.

Paralectotypes

(1) Slab 17.1.12. The three specimens remaining on this slab after selection of the lectotype. One of these, B.M. 1961.12.6.53, has opercular valves but no animal parts, the other two are empty shells. Other details as above.

(2) Shell 18. This is Darwin's figured specimen (Darwin, 1854, Pl. 5, *2d*), from a ship from West Africa. Stubbings (1959) describes the distorted condition of the specimen and gives good reason for believing the distortion to be due to the toxic effect of the copper sheathing of the hull to which it was attached. B.M. 1961.12.6.49c.

(3) Shell No. 8. A well-formed empty shell very similar in appearance to those on Slab 17.1.12, " ship from west coast of Africa ". B.M. 1961.12.6.50c.

(4) Shells 9, 10, 14, 16 are all empty shells distorted in their growth and very similar to Shell 18. All from a ship or ships from West Africa. Shell 9, B.M. 1961.12.6.55c, had a second broken specimen attached which has been sectioned B.M. 1961.12.6.55d. Shell 10, B.M. 1961.12.6.55e, is a small specimen attached to a piece of mollusc shell with another white barnacle shell alongside it. Shell 14, B.M. 1961.12.6.34e carries three specimens of *B. venustus* as noted in Darwin's M.S. Shell 16 is registered B.M. 1961.12.6.54c.

(5) Shell 12, B.M. 1961.12.6.57c, a whitish empty shell from West Africa.

(6) Slab 17.1.28, B.M. 1961.12.6.58c. Three or four of the specimens half buried under specimens of another species, *B. tintinnabulum*. On the back of the slab in Darwin's writing is " *B. tint.* with *B. amphitrite* var. *stutsburi*", and also written in the same hand at another time " *B. subcostatus* Leach, W. Indies, Rev. L. Guilding ". *B. subcostatus* appears to be a manuscript name.

(7) Microscope Slide No. 23 of the University Museum of Zoology, Cambridge. Listed in Darwin's writing as " *amphitrite stutsbury* single specimen " and containing mouth-parts, labrum and cirrus. The mounting medium on the slide was badly shrunk and dark brown in colour, but it has been possible to remount the specimen in polyvinyl lactophenol and the principal parts have been photographed (Pl. 5, *b*, *d*).

(8) Opercular Valves 9. B.M. 1961.12.6.59e, two scuta and four terga.

(9) Opercular Valves 10. B.M. 1961.12.6.60e, one scutum and one tergum.

[Shell No. 17 is listed as " var. *stutsburi* West Africa ". This was a complete specimen but with the shell very much distorted by crowding and from the shell alone difficult to determine. Examination of the opercular valves, labrum and 3rd cirrus leave no doubt that it is not *stutsburi* but a specimen of *Balanus amphitrite* s. str.]

The lectotype is a very fine and typical specimen, one of the few in the type collection with the shell undistorted in its growth and the only one complete with animal parts as well as valves and shell, but I have hesitated before selecting it as it comes from the West Indies, and Darwin wrote (Darwin, 1854, 246), " all the specimens which I have seen have come on shells or on ships' bottoms, from West Africa ". Now Darwin must have seen not only the lectotype but also the specimens on Slab 17.1.28 which are also from the West Indies, for the slabs have his writing on the back. He may not have known that the lectotype and others on Slab 17.1.12 came from the West Indies ; but Slab 17.1.28 has " West Indies " and also " var. *stutsburi* " in his own writing. I am indebted to my colleague Miss B. M. Skramovsky for confirming that the writing is Darwin's. It is therefore my duty under Recommendation 72E of the International Code of Zoological Nomenclature (Stoll *et al.*, 1961) to correct the type-locality, erroneously restricted to West Africa, to include the West Indies. Having done so I am free to select the lectotype designated above.

DESCRIPTION

Size. The greatest diameter of the base of the lectotype is 17·3 mm. and its height is 9·5 mm. Specimen B of this group measures 18·5 mm. and 11·1 mm. respectively and a third specimen 18·6 mm. and 12·6 mm. The specimen of Darwin's figure *2d* is smaller—11·3 mm. in diameter and 8·1 mm. high.

Colour. The upper part of the shell is usually white and the lower part coloured by pinkish purple stripes which coalesce.

The radii are conspicuously white and have oblique summits.

Shape. The undistorted specimens are conical with a straight rostrum and straight or concave carina, the carina being distinctly higher than the rostrum.

The parietes. The photographs (Pl. 4, *g*, *h*) show sections of parietes which seem to be typical of this subspecies and very similar to sections of *pallidus*. In addition to the normal row of large pores there are subsidiary small pores outside them more or less opposite the septa. Immediately around the pores the shell substance is white and outside both the large and small pores there is in those parts of the shell where the coloured stripes coalesce a crescent of purple colour. Between each pore and the inner face of the parietes there is in section a white line parallel to the plane of the wall and about the length of the width of the pore. The " tree-like " pattern is rather obscure in the specimen photographed but the elements are there and in other specimens examined they are more like those specimens of *B. amphitrite* s. str.

The radii have inconspicuous denticles to the lower edge of the septa on the sutural margin. The shell material filling the interspaces is more hyaline than the opaquely white septa.

The scutum of the lectotype (Pl. 4, *c*, *d*) and the others from Slab 17.1.12 have externally a dark blue-black triangular area bounded by white borders on the scutal and occludent margins. The growth lines are moderately developed, the roughness of the inner surface of the apical part of the valve between the articular ridge and the occludent margin is in the form of rough longitudinal ridges. The base of the articular ridge continues towards the base of the valve as a low rounded ridge passing very near to the shallow impression of the lateral depressor muscle and between this and the adductor ridge is another faint ridge.

The tergum usually has a long and narrow spur at about its own width distant from the basi-scutal angle (Pl. 4, *e*, *f*). The crests for the lateral depressor muscle are well developed and project beyond the basal margin. In addition to the growth lines the external surface shows some longitudinal striations which correspond with the crests for the lateral depressor muscles on the other side of the valve.

The labrum of specimen A (Pl. 5, *a*) has only one tooth on each side. That of Darwin's dissection now in the University Museum of Zoology, Cambridge (Pl. 8, *b*) has three and I believe this to be the more normal condition.

The mandible is shown in Pl. 5, *e*, but I can see nothing remarkable about it.

The maxilla of specimen A (Pl. 5, *c*) has weakly developed spines, the two pairs of strong spines being hardly larger than the others. That of the University Museum of Zoology, Cambridge specimens (Pl. 5, *d*) also has rather weaker spines but I have seen maxilla of this subspecies with normally developed spines.

The cirri are shown in Pl. 5, *f*, *g*, *h*, *i*, the 3rd cirrus has very short, broad segments and is very hairy (Pl. 5, *h*, *k*).

Apart from the colour difference I have been unable to find a satisfactory way of distinguishing *stutsburi* from *pallidus*. The following features are characteristic of both and usually separate them from the other forms: the very long spur to the tergum, the presence of supplementary pores in the parietes and the triangular dark patch on the scutum. In order to draw attention to the similarity I am, in this paper, treating them as belonging to the same species. Unfortunately, the rules do not permit the name of this species to be *stutsburi* with *pallidus* as its pale subspecies, for the name *pallidus* has line priority over *stutsburi* in Darwin's monograph. The name of the species must therefore be *Balanus pallidus* and *stutsburi* is a coloured subspecies.

Balanus venustus venustus Darwin

Balanus amphitrite var. *venustus* Darwin, 1854, p. 250, pl. 5, fig. 2*a*.

Lectotype. Pl. 6, *a–g*, *j–p*. A complete specimen, Reg. No. B.M. 1961.12.2.24c, selected from the same piece of bamboo as the lectotype of *Balanus amphitrite* s. str. The shell was growing on a specimen of the latter sub-species and remains there but the opercular valves have been removed and mounted on a slide (Reg. No. B.M. 1961.12.6.24a) and the animal parts have been dissected and mounted in polyvinyl lactophenol on a second slide, Reg. No. B.M. 1961.12.6.24b. Locality: Natal, Dr. Krauss.

Paralectotypes

(1) About fifteen other small pink barnacles on the main piece of bamboo. The shell of one of these B.M. 1961.12.6.25d, is sectioned and shown in Pl. 3, *d* (there are no specimens of this subspecies on the second, shorter piece of bamboo).

(2) Specimens on Slab 17.1.21 (Reg. B.M. 40.9.30.64–65) : B.M. 1961.12.6.26e, a group of four, two of them complete with opercular valves and one perhaps still with animal parts ; a particularly well grown separate specimen without valves; three separate scuta ; four terga and three parietes one of which, B.M. 1961.12.6.26d, had been sectioned. Locality : Good Hope, Dr. Krauss.

(3) Shell 15. A large specimen from Ceylon without valves, B.M. 1961.12.6.27c.

(4) Shell 19. A specimen, B.M. 1961.12.6.28c, listed as " var. *venustus* (with var. *communis*) Natal ", there is no sign of the var. *communis* now. No valves.

(5) Shell 20. B.M. 1961.12.6.29c. Listed as " do. on an *Ostrea* ". (" do." being the abbreviation for " ditto " for " var. *venustus* "), but there is no sign of the oyster. No valves. Natal.

(6) Shell 30. B.M. 1961.12.6.30c. This is the specimen of the " var. *venustus* " figured in Darwin's monograph (Pl. 6, 2*a*), although according to the list it is " var. *communis* ", clearly the correspondence between the present arrangement of the specimens and the list is imperfect.

(7) Opercular valves 5. A scutum and a tergum. B.M. 1961.12.6.31e.

(8) Opercular valves 13. A scutum, Natal. B.M. 1961.12.6.32e.

(9) Slab 17.1.30. Reg. No. B.M. 1961.12.6.33e. Several specimens mostly empty on two conical mollusc shells. Locality : Algoa Bay, Dr. Stanger. One sectioned, B.M. 1961.12.6.33d.

(10) Shells 14. Two empty shells, B.M. 1961.12.6.34c, on a specimen of *Balanus amphitrite stutsburi*. Ship's bottom from West Africa.

(11) Shell 17. Two small complete specimens B.M. 1961.12.6.35c on a specimen which is listed as *B. amphitrite stutsburi* from West Africa ; but is in fact *B. amphitrite* s. str.

I have selected the lectotype from the material on the bamboo as there are more specimens here than in any other group to choose from. The specimens were undoubtedly seen by Darwin and although he has left no definite indication of naming them var. *venustus* he must have recognized them and considered them when writing his monograph, and they will be the specimens of this variety from Natal associated with var. *communis* which he refers to on p. 246.

DESCRIPTION

Size. The greatest diameter of the base of the lectotype is 8·9 mm. None of the other specimens on the bamboo is as large as this. By far the largest specimen is Shell No. 15 from Ceylon with the basal diameter of 14·8 mm. The next in size is one on Slab 21 from West Africa which measures 10·9 mm. Nearly all the other specimens in the collection are smaller than the lectotype.

Colour. The ground colour is white or slightly pinkish and the walls are ornamented with about forty evenly spaced stripes. The stripes of the lectotype are purplish pink. Shell No. 30 (the specimen of Darwin's fig. 2*a*) is of a paler pink and considerably paler than it is represented in the coloured figure of the monograph. Some of the paratypes on the bamboo however have stripes of as dark a red as this figure shows.

The radii of the lectotype are of the same colour near the parietes as the stripes, becoming gradually paler towards the edges. Most of the radii are coloured in this way but sometimes the pinkish colour near the parietes is broken up into one or two stripes. In contrast to the position in *B. amphitrite* s. str. any colour in a radius of *venustus* is in the material filling the interspaces between the septa which are themselves white in colour.

Shape. The profile of the rostrum is nearly always convex and that of the carina is usually concave. The summits of the radii may be parallel to the base but often they are oblique leaving the upper parts of the alae exposed.

Parietes. An immediate difference between *Balanus venustus* and *Balanus amphitrite* becomes apparent if a section of a parietal wall is examined (Pl. 6, *h*) ; the coloured stripes come opposite the septa between the pores instead of opposite the pores themselves. Otherwise the pattern visible on the polished surface of a section is very similar in the two species. There are the same tree-like outgrowths running into the ribs from the white line running down the middle of the septum. The other, outer, end of this line often runs into the pink patch which is the section of the stripe, bifurcating it on its inner side. On the sutural edges of the radii the septa have conspicuous denticuli projecting from their lower sides. Unless care is taken with the illumination when examining the edge of the radius, the shadows cast between the denticuli make it difficult to see that the spaces between the septa are filled up solidly ; and the fact that the filling material is often more darkly coloured than the septa adds to this difficulty.

The scutum of the lectotype is shown in Pl. 6, *d*, *e*. It is very similar to that of *Balanus amphitrite* but has a distinct tinge of purple colour in its substance. This colour in some of the paralectotypes is pink rather than purplish. The articular ridge is more than half the length of the outer margin and continues towards the base as a low ridge well clear of the pit for the lateral depressor muscle.

The tergum differs in colour from that of *Balanus amphitrite* s. str. in the same way as the scutum. The spur is much closer to the scutal margin and the carinal half of the valve is less developed than the scutal half so that the carinal edge is very much shorter than the scutal edge, or in Darwin's words, " The carinal half of the basal margin is much hollowed out ". The crests for the depressor muscles are well developed and project beyond the margin, they have been damaged in the lectotype (Pl. 6, *f*, *g*).

The labrum of the lectotype (Pl. 6, *c*) has three large teeth on each side and the notch is smooth.

The mandible and maxilla (Pl. 6, *n*, *o*) have no special features distinguishing them from those of *Balanus amphitrite* s. str., except that the maxilla has only five small spines between the two pairs of large spines.

Four of the six pairs of cirri are shown in Pl. 6, *j–m*, but the only difference I could find between these and those of *B. amphitrite* was in the 3rd cirrus (Pl. 6, *p*) which appears to lack the curved spines on the inner and outer faces.

Balanus venustus niveus Darwin

Balanus amphitrite var. *niveus* Darwin, 1854, p. 240, pl. 5, fig. 2*f*.

Lectotype. (Pl. 7, *a*, *b*, *d–h*, *l–r*.) One of the specimens on Slab 17.1.29. Reg. No. B.M. 40.4.5.59, now registered B.M. 1961.12.6.61c. The animal parts were still inside this shell and have now been dissected and mounted on a slide, Reg. No. B.M. 1961.12.6.61b. The valves had, however, been removed but are presumably those mounted separately on the same slab. These are now on a separate slide, Reg. No. B.M. 1961.12.6.61a. Locality: Madagascar.

Paralectotypes

(1) A group of five B.M. 1961.12.6.62e fully grown and two very much smaller specimens on the same slab (17.1.29). Two of these have no opercular valves and none has animal parts. The parietes of one of this group have been sectioned. B.M. 1961.12.6.62d.

(2) " Shell " 32. An empty shell which is the specimen on pl. 5, fig. 2*f* in Darwin's Monograph; from the West Indies. B.M. 1961.12.6.63c.

(3) Shell 33. Part of a large specimen consisting of the rostrum, the right lateral and some of the basis, from Madagascar. B.M. 1961.12.6.64c.

(4) Shell 36. A whitish shell without opercular valves, from Madagascar. B.M. 1961.12.6.65c.

(5) Shell 35, an empty shell listed as " var. *niveus*, coast of Portugal ". B.M. 1961.12.6.68c.

Other material

(1) Shell 31, an empty shell very similar to Shell 32 and certainly a *niveus* but not strictly a paralectotype as position 31 is listed as " var. *communis* ". This shell has provided the sections shown in Pl. 7, *j*, *k*. B.M. 1961.12.6.66d.

(2) Shell 34, a very similar empty shell to Shell 31 and also listed as *communis*. B.M. 1961.12.6.74a.

(3) Opercular valves 12, a scutum and a tergum. B.M. 1961.12.6.67e. According to the list these are " var. *niveus* (West Indies) ", but they do not seem to be typical.

The only specimen with animal parts has been chosen as the lectotype and the opercular valves which were mounted beside them are assumed to have come from this specimen.

DESCRIPTION

Size. The greatest diameter of the lectotype is 8·4 mm. The length of the left lateral 8·2 mm. and the right lateral 4·3 mm. The basis of the largest paratype measures 11 mm. but the two parietes left of Shell 35 must have belonged to a larger specimen than this.

Colour. All the specimens are white with numerous narrow colourless hyaline stripes. The opercular valves of the lectotype are white with traces of deep purple coloured epidermis on the inside. The opercular valves No. 12 mounted by Darwin have a slightly bluish tinge and the traces of epidermis are a dark blue-grey.

Shape. Very similar to that described above for *B. amphitrite* s. str. and for *B. venustus venustus* but the summits of the radii of all the specimens are oblique.

Parietes. A polished section of a piece of parietes (Pl. 7, *j, k*) shows a pattern basically as that of *B. amphitrite* s. str., but there is no colour and the narrow hyaline stripes of the shell correspond to the septa between the pores.

The sutural edges of the radii of " Shell 33 " have distinct denticuli on the lower sides of the septa. The septa are of a more opaque-white than the shell substance filling the interspaces.

The scutum. (Pl. 7, *f, g.*) The angle between the tergal and basal margins is rather sharp in the right scutum of the lectotype and less so in the left. The articular ridge is more than half the length of the tergal margins and the slight ridge running from it curves asymptotically to the basal margin away from the pit for the lateral depressor muscle. The scutum of Opercular Valves 12 has a very short articular ridge considerably less than half the length of the total margin and the ridge running from it between the basal margin is very faint and there is no pit for the lateral depressor muscle.

The tergum (Pl. 7, *d, e*), which is presumably from the lectotype has been damaged. It is very like that of *B. amphitrite venustus* with the spur close to the scutal margin and the carinal half of the basal margin much hollowed out. The crests for the depressor muscles project well beyond the basal margin. The tergum of Opercular Valves 12 has a long and narrow spur and the crests for the depressor muscles are hardly developed.

The labrum and mandible (Pl. 7, *l, h*) are very similar to those of *B. amphitrite venustus.* The labrum of the lectotype has three teeth on each side. The maxilla of the lectotype (Pl. 7, *m*) has the lower part of the inner edge slightly protuberant and bears the lower two large spines. The angle below this is square. There are five smaller spines between the two large pairs of spines.

The cirri of the lectotype (Pl. 7, *n–r*) call for no special comment.

The rami of the 3rd cirrus bear curved hooks (Pl. 7, *r*) rather like those of *Balanus amphitrite.*

Balanus venustus modestus Darwin

Balanus amphitrite var. *modestus* Darwin, 1854, p. 240.

Lectotype. (Pl. 8, *a, b, d–p.*) A specimen selected from a group of barnacles on the shell of a fasciolariid gastropod mounted on Slab 17.1.19. The barnacle is complete with opercular valves and animal parts. The shell Reg. No. B.M. 1961.12.6.69e remains on the mollusc shell but the valves are now separated (Reg. No. B.M. 1961.12.6.69a) and the dissected appendages are on a microscope slide Reg. No. B.M. 1961.12.6.69b.

Locality probably the West Indies area or the American coast from Florida to Texas.

Paralectotypes

(1) About 20 other specimens on the same gastropod shell B.M. 1961.12.6.70e. Only three or four of these still have the opercular valves and there are also specimens of *B. amphitrite niveus* amongst them. The parietes of one of these paratypes has been sectioned. B.M. 1961.12.6.71d and B.M. 1961.12.6.72d.

(2) Two empty shells on the upper valve of an oyster shell, B.M. 1961.12.6.73c, the lower half of which is still on the fasciolariid shell referred to above. These two shells are listed by Darwin as " Number 27 var. *modestus* on a univalve ".

(3) Opercular Valve 8. One tergum. B.M. 1961.12.6.84.e

(4) Cambridge microscope slide 158 with mouth parts and cirri dissected and mounted by Darwin now in the Museum of Zoology, Cambridge ; listed by Darwin as " 158. *B. modestus* var. of *B. amph.* ? do. - do.". The " do. - do." refers to " 1, 2, 3, 6 cirri . . . all trophi ".

All this material is from the one source : barnacles growing on the fasciolariid gastropod from a locality unknown to Darwin. My colleague, Mr. S. P. Dance, has however kindly examined the mollusc shell for me and has been able to identify it as *Leucozonia nassa* Gmelin, a species which is common among rocks at low tide from Florida to Texas and the West Indies.

DESCRIPTION

Size. The lectotype cannot be measured accurately as it is too closely surrounded by other specimens. The greatest dimension of the base is about 7·5 mm. The largest specimen reaches 8 mm. in basal diameter.

Colour. In Darwin's words, " Upper part of shell white, lower part uniformly bluish-grey ". Most of the specimens including the lectotype show no trace of stripes but a few specimens have the bluish-grey colour confined to narrow vertical stripes. The bluish-grey colour is confined to the parietes, and valves and radii are white. There is a tendency for all the parietes including the carina to have convex profiles so that the shell has the shape of an inflated, truncated cone.

The radii are broad with oblique summits. Many of the specimens but not the lectotype have a conspicuous ribbing parallel to the base on the external surface of the radii.

Parietes. A polished section of a parietes is very similar to one of *B. amphitrite* s. str. (Pl. 8, *c*). If the example is one without stripes the bluish-grey colour of the shell permeates most of the shell substance. A stripe, if any are present can be seen in section in addition to the bluish-grey background as a crescent of dark purple brick colour embracing the outer half of the section of a pore.

I have not been able to examine the sutural edges of more than one or two radii where the septa were seen to have inconspicuous denticuli in the lower sides. The septa were more opaquely-white than the substance filling the spaces between.

The scutum of the lectotype (Pl. 8, *d*, *e*) has an articular ridge distinctly longer than half of the scutal margin and from it a slight ridge runs towards the basal margin between the pit for the lateral depressor muscle and the adductor ridge. The tergal margin makes a distinct though obtuse angle with the basal margin.

The pit for the lateral depressor muscle is small but deep and opens on to the basal margin.

The tergum of the lectotype (Pl. 8, *f*, *g*) has a short spur near to the scutal margin. The crests for the depressor muscle extend beyond the scutal margin. The internal surface is roughened.

The labrum (Pl. 8, *p*) has three teeth on each side, two of them being close together on the edge of the notch.

The mandible (Pl. 8, *k*) has a rather large upturned 3rd tooth.

The maxilla (Pl. 8, *j*) has five spines between the two pairs of large spines and the spines of the lower large pair are a little larger than those of the upper large pair.

Four cirri of the lectotype are shown in (Pl. 8, *k*, *l*, *m*, *n*) with an enlargement of part of cirrus 3 in Pl. 8, *o*. The spines on the inner and outer faces of this cirrus are similar to those of *B. amphitrite* s. str. but less conspicuous.

Balanus venustus obscurus Darwin

Balanus amphitriate var. *obscurus* Darwin, 1854, p. 241, pl. 5, fig. 2*g*.

Lectotype (Pl. 9, *a–n*, *q*) a specimen on a segment of crustacean limb from Slab 17.1.22, which was complete with opercular valves and animal parts. Locality, Jamaica, Mus. Leach. Reg. Nos. Shell B.M. 1961.12.6.75c, valves B.M. 1961.12.6.75a, animal parts, B.M. 1961.12.6.75*b*.

Paralectotypes

(1) Three other specimens on the same slab also complete with valves and possibly animal parts, also one parietal wall and two terga. B.M. 1961.12.6.76e.

(2) Three parietes from the slab kept separately B.M. 1961.12.6.c.

(3) Two further parietes from the same slab which have been sectioned B.M. 1961.12.6.76d and B.M. 1961.12.6.77d.

(4) Shell 23 listed as " var. *obscurus* on patella local. Unknown ". All that remains now is three separate pieces of parietal wall, B.M. 1961.12.6.78a, and one that has been sectioned, B.M. 1961.12.6.78d.

(5) Slab 17.1.3. Eleven specimens on a pebble from an unknown locality " M. Cuming ". B.M. 1961.12.6.79c.

There are some specimens in Darwin's list which are not now available. " Shell 38 var. *obscurus* hab. unknown C.D." is now missing, and none of Opercular Valves 14 remains. Shells 26 are undoubtedly of *Balanus perforatus* and cannot be the original specimen of " var. *obscurus* loc. unknown " that Darwin placed here.

I have chosen the specimen on the segment of crustacean limb for the lectotype as it is one of the complete specimens from a known locality and is a specimen which is easily specified, it also agrees very well with Darwin's description.

Size. The base of the largest intact specimen which is the lectotype has a greatest diameter of 6·7 mm. The specimens on a pebble are too crowded to be measured, but at least three of them are 12 mm. across or more.

The colour of the lectotype is pale grey with narrow dark grey longitudinal stripes.

There are more stripes near the basis of the shell than near the orifice for two reasons : (i) there is a tendency for the stripes to be split towards the base, and (ii) for additionally thin lines to appear between them. There is sufficient contrast between the ground colour of the stripes for the latter to be quite distinct in the lectotype and other shells on Slab 17.1.22; but the parietes of Shell 23 have very indistinct stripes and the contrast between the background and the stripes is very slight ; the central portions of the wall are dark and parts near the margins, particularly near the basis are pale. The background colour of the central portion is much darker than are the stripes of the pale marginal portions.

The radii which have summits at about 45° are closely ribbed horizontally and also ribbed to a lesser extent vertically. The small rectangles between the vertical and horizontal ribs are often reddish in colour, the ribs themselves being white.

The shape is very similar to that described above for *venustus* and *niveus* but the orifice is rather small.

The parietes. The horizontal section of parietal wall near the base (Pl. 9, *o*, *p*) shows that there are here more stripes than there are pores. There is a stripe opposite each septum and in addition there are usually thinner stripes between these. There are the usual white lines running down the middle of each septum from the coloured patch-like section of a stripe at one end to the tree-like pattern in the internal rib, at the other end. A similar white line runs from each of the subsidiary stripes inwards towards the pore and leads to a smaller tree pattern in a rib not in the inner wall but inside the pore itself. The pores are thus partly divided into two by subsidiary ribs. Sometimes there are two such ribs in a single pore dividing it into three. Each stripe therefore corresponds to a rib and the rib may either be in the normal place on the inner wall of the parietes or it may be inside a pore.

In addition to the pattern so far described there are often crescents of reddish brown similar to those of *modestus* outside the pores or portions of pores. These crescents can be seen in Pl. 9, *p* ; the clearest example being opposite the middle portion of the tripartite pore in the centre of the picture. The pattern in *obscurus* is interesting as it combines the pattern of *amphitrite* s. str. with that of *venustus* s. str. Like *venustus* the stripes seen on the outside of the shell correspond with the septa between the pores and like *amphitrite* the pores have pigment outside them, only in *amphitrite* this pigment is seen from the outside as stripes and in *obscurus* it is too deep to show externally.

The sutural edges of the radii of the disarticulated Shell 23 have very conspicuous, and occasionally ramifying denticuli on the lower sides of the septa. The septa are white and the substance filling the interspaces is pale bluish-grey, like the stripes of the shells. The denticuli are very inconspicuous in other specimens.

The scutum of the lectotype (Pl. 9, *c*, *d*) has a very long articular ridge more than two-thirds the length of the tergal margin ; otherwise it is very similar to that of *venustus* or *niveus*.

The tergum of the lectotype (Pl. 9, *e*, *f*) is also very similar to that of *venustus* and *niveus* with the spur very close to the scutal margin and the carinal half of the valve much less developed than the occludent half.

The labrum (Pl. 9, *n*) of the lectotype has three teeth on each side of the notch, the two inner teeth being closer together. The labrum again shows no difference between this form and *venustus* and *niveus*.

The mandible and maxilla (Pl. 9, *e*, *m*) call for no special comment. There are five spines between the two large pairs of large spines on the maxilla.

The cirri as shown in Pl. 9, *g–k* are very similar to those of *niveus*. The details of the 3rd cirrus of *obscurus* are so similar to those of *niveus* that I have had to re-examine the specimens to make sure that the photographs of the 3rd cirrus of *obscurus* (Pl. 9, *q*) and of *niveus* (Pl. 7, *r*) are really of these two forms respectively and not, as could easily be thought, two photographs of the same specimen.

Balanus variegatus Darwin

Balanus amphitrite var. *variegatus* Darwin, 1854, p. 241.

Lectotype

A large specimen on Slab 17.1.31 from Sydney with opercular valves loose in the shell but no animal parts (Pl. 10, *a*). This specimen was first labelled by Darwin " var. *cirratus* " in ink but this has been crossed out in his writing in pencil and " var. *variegatus* " substituted. This specimen had 187–40.9.22.283 in ink written on it but I can find no trace of this in the Museum register.

The specimen has been re-registered : the parietes and base, B.M. 1961.12.6.80e ; the valves, B.M. 1961.12.6.80a, and the sectioned wall which is from the same specimen, B.M. 1961.12.6.80d.

Paralectotype

(1) Material on microscope slide No. 151 of the Zoology Museum, Cambridge. This is in rather poor condition but with the mouth-parts and a few cirri clearly visible (Pl. 10, *g–k*). This is listed by Darwin as " 151 *B. variegatus* do. – do.". The " do. – do." being an abbreviation for " 1, 2, 3, 6 cirri . . . all trophi ".

(2) Opercular Valves No. 16. A broken scutum and a tergum from New Zealand. B.M. 1961.12.6.81e.

Other material

1. Slab 17.1.33. B.M. 1961.12.6.87e. Labelled by Darwin " *B. amphitrite* var. between *obscurus* and *variegatus* ". Four shells complete with opercular valves and probably animal parts, one of these has now been dissected, four empty shells, one of which I have sectioned, two parietal walls, four scuta and one tergum.

(2) Shell 24. B.M. 1961.12.6.88c listed as " do. passing into var. *variegatus*. Ship's bottom taken in E. Australia ", the "do." being " ditto " for " var. *obscurus* " in the line above. An empty shell very similar to those on Slab 17.1.33. These are all undoubtedly the specimens from H.M.S. " Fly " referred to by Darwin (1854, p. 246).

DESCRIPTION

Size. The greatest diameter of the specimen from Sydney is 17 mm. The specimen from which the appendages on the slide in the Cambridge Museum were taken must have been much smaller than this.

Shape. The only specimen now available is not typical as Darwin describes the shape as conical and this specimen is rather barrel-shaped. The summits of the radii are oblique.

Colour. The ground colour of the shell is cream with a tinge of pink and the numerous stripes are slaty blue at the base, becoming claret red between the basis and freckled with cream transversely in the way shown in the photograph.

Parietes. The section of a right lateral near the base is shown in Pl. 10, *f*, the pores are numerous, round and even, and the pattern of the polished shell of the section is much like that of *B. amphitrite* s. str. with the pigment rather broken up as might be expected from the freckled nature of the stripes.

The sutural edges of the radii have short, blunt denticuli on the lower sides of the septa. There are flecks of purple in the material which fills up the interspaces but the septa themselves are white.

The scutum (Pl. 10, *b*, *c*) has a short but distinct adductor ridge. The pit for the lateral depressor muscle is deep and well defined but is open towards the basal margin. Externally there are longitudinal striae as well as the transverse growth lines.

The tergum (Pl. 10, *d*, *e*) has a moderately short spur which tapers slightly and is well away from the basiscutal angle. The crests for the depressor muscles are comparatively few in number and rather short.

The mouth-parts can be described only from the Cambridge specimen.

The labrum (Pl. 10, *g*) has three teeth on each side of the notch.

The maxilla (Pl. 10, *i*) has the lower part which bears the lower of the two pairs of large spines forming a distinct projection of the inner edge. The first and second cirri and parts of other cirri, which is all there is preserved on the slide, show no special features.

I have also examined the material from H.M.S. " Fly " referred to above, which Darwin considered to be intermediate between *obscurus* and *variegatus* and which therefore cannot be treated as type material for *variegatus*.

To me these specimens belong to *B. variegatus*, all five of the terga I have examined are very like those of the lectotype of this species. The stripes on the shells are broken up into flecks of colour and one of the maxillae of the dissected specimen has a projecting lower portion of the inner face. Darwin did not give his reasons for placing these specimens near to *obscurus* presumably because of the rather numerous dark grey stripes on a paler grey background. The colour alone is not in my opinion sufficient to indicate affinity with *obscurus* in the absence of other evidence and in the face of the difference in the tergum, and as regards the numerousness of the stripes this is a character shared with *B. variegatus* (see Pl. 10, *a*). Examination of the ground section of the shell of one of these H.M.S. " Fly " specimens also supports my view that these can be identified as *B. variegatus*. The pores are all simple—one to each stripe and not subdivided as they are in *B. venustus* *obscurus* and the colour of the flecks in the shell substance opposite the pores is reddish purple as it is in *B. variegatus*. *B. venustus obscurus* only has grey here. The mandible is rather different from either and so is the labrum which in the dissected specimen has four teeth on each side.

Balanus variegatus var. ***cirratus*** Darwin

Balanus amphitrite var. *cirratus* Darwin, 1854, p. 241, pl. 5, fig. 2*b*.

Lectotype (Pl. 10, *l*) a large specimen on a gastropod shell on Slab 17.1.35 without opercular valves or animal parts, with Darwin's writing on the back of the slab " *Bal. amphitrite* var. *cirratus*. Mouth of Indus ", B.M. 1961.12.6.82c.

Paralectotypes

(1) Slab 17.1.35. Five empty shells without valves on a second gastropod on the same slab as the lectotype. B.M. 1961.12.6.82e.

(2) Slab 17.1.16. About half a dozen empty shells and parts of shells on a similar but larger gastropod shell (Pl. 10, *m*). B.M. 1961.12.6.82e. " *Bal. amphitrite* var. *cirratus*. Mouth of Indus ".

None of the specimens has valves or animal parts and Shell 37 of Darwin's list is now missing.

Size. The greatest basal diameter of the largest specimen is 13·5 mm. The colour of most of the shells is buff rather than " very pale purplish brown " described by Darwin, with " indistinct longitudinal brownish stripes transversely flecked with white ". The brown colour in most cases being approximately that of medium oak. The lectotype has, however, a distinctly pink tinge.

The shape of the shell is similar to that of *B. venustus* with a convex rostrum and a concave carina, the latter often projecting slightly outwards like the spout of a jug. None of the present specimens have the cup-like bases that Darwin described as being typical of the variety.

The radii have oblique summits and are usually horizontally ribbed with slaty-blue lines. I have been unable to see the sutural edges of the radii well enough to be able to describe the septa.

The parietes. As Darwin remarks the walls are thin and a section of the parietes shows that the pores are comparatively large. The pattern seen on the polished surface of the section is of the normal type of *B. amphitrite* s. str. with the stripes coming opposite the pores. As seen in Pl. 10, *n*, the pattern between the pores and the outer face is broken up in places by opaque white flecks running inwards from the outer surface. These seem to correspond with the transverse freckles of white on the shells.

All that remains of Darwin's material is quite inadequate for a proper description of *cirratus*. Not only are there no valves or animal parts but none of the specimens now available have the cup-formed shape of the bases. Darwin when discussing his decision to place the various varieties under the one specific name *B. amphitrite* wrote that he had more doubt regarding the *cirratus* than on any other and was inclined to give it separate specific status; but to me there is very little or no difference between it and *variegatus*.

The peculiar features Darwin stresses are:

1. The peculiar colour. 2. The bases having the cup-formed shape. 3. Beaded growth lines on the scuta. 4. He also notes that the maxillae have the corner extremely prominent.

To take these in turn: 1. The colours of the specimens now extant with Darwin's own written identifications of *cirratus* and *variegatus* overlap. 2. None of the specimens of *cirratus* has the peculiar cup-formed basis, but the specimen of *variegatus* Pl. 10, *a*, has. 3. Beaded growth lines on the scuta might provide a valid difference though Darwin writes that he has seen traces in the common variety. Unfortunately there are no scuta of *cirratus* now available for study. None of the specimens labelled *variegatus* has beaded scuta. 4. The prominent lower corner of the maxilla does not separate *cirratus* from *variegatus* for the latter, like specimens of *niveus*, tends to have a maxilla like this.

No one who has worked on barnacles during the last hundred years can have failed to be impressed by the quality of Darwin's monumental work and it seems anomalous that I should be unable to distinguish his var. *cirratus* from his var. *variegatus* especially as *cirratus* was the variety he was most inclined to separate from all the others and raise to specific rank. The discrepancy can only be accounted for by the absence today of sufficient type material. Of the var. *cirratus* only empty shells remain and as Darwin emphasized repeatedly, sessile cirripedes cannot be identified satisfactorily without an examination of the opercular valves.

DISCUSSION

In this paper I have divided Darwin's varieties of *Balanus amphitrite* into four separate species. This seems to be the simplest way of expressing my views concerning the affinities between them. First there is *Balanus amphitrite* itself characterized by the presence of numerous teeth on the labrum running down into the notch and by a short stout spur to the tergum not very close to the basi-scutal angle. Secondly, *Balanus pallidus* characterized by a very long spur to the tergum with *B. pallidus stutsburi* as a coloured variety or subspecies. Thirdly, *Balanus venustus* with *niveus*, *modestus* and *obscurus* as three of its subspecies, all with very similar and characteristically shaped terga with a short spur near the basi-scutal angle and hollowed out carinal half of the basal margin. Fourth and last *Balanus variegatus* is less easy to place, it differs from *B. amphitrite* in the teeth of the labrum and lacks the characteristic shape of tergum possessed by *B. venustus* and its subspecies. Darwin's var. *cirratus* I have treated as a variety of *B. variegatus* with beaded scuta, on the basis of Darwin's description, the type material is inadequate for a separation.

Concerning the characters used to separate the subspecies, the external colour pattern of the shell and the relationship of this pattern to the underlying shell structure are important. In some such as *B. amphitrite* the pores in the parietes lie underneath the coloured stripes on the outside and in others such as *B. venustus venustus* the pores are between the stripes. The radii are usually white but colour or texture differences between the substance of the septa and the material filling the spaces between them is of interest especially when considered in relation to the colours seen on the surface or inside the substance of the parietes. There is a tendency for the colour opposite a septum of a parietal wall to be similar to the colour of the interseptal material of a radius (see Table I).

TABLE I.—*Colours Seen in Section of Parietes and Radii*

	Parietes		Radii	
Name	Opposite septa	Opposite Pores	Substance of septa	Substance filling interspaces
amphitrite	Off white	Dark slate with tinge of violet	Off white or with flecks of colour	Off white.
venustus	Purplish pink	White or slightly pinkish	Whitish	Purplish pink.
pallidus	White	White	Opaquely white	Hyaline white.
stutsburi	Upper part white, lower part mostly white	Upper part white, lower part purple pink	Opaquely white	Hyaline white.
niveus	Hyaline white	Opaque white	Opaquely white	Hyaline white.
modestus	Upper part white, lower part white or bluish-grey	Upper part white, lower part bluish-grey or reddish brown in section	Opaquely white	Hyaline white.
obscurus	Dark grey	Pale grey	White	Pale bluish-grey or reddish.
variegatus	Bluish-grey with white or cream flecks	Bluish-grey with purple flecks	Cream with a few purple flecks	Cream.
cirratus	Flecks of dirty pink	White	Not seen	Not seen.

The pores themselves although very variable in most forms are very characteristic in *B. venustus obscurus*, where they are partially subdivided by a rib growing in from the outer lamina of the shell. The presence of subsidiary pores seems to be a feature of *B. pallidus* including its subspecies *stutsburi*.

The tergum is of greater diagnostic value than the scutum and the four species can usually be separated by its shape alone.

The labrum is very valuable for separating *B. amphitrite* from the rest ; but is of little further value.

The maxilla of *B. venustus venustus*, *B. venustus niveus* and *B. variegatus* tends to have the lower part of the inner edge slightly protuberant ; but this is a variable character and the lectotype of *B. venustus niveus* hardly shows it.

The only cirrus to provide useful characters is the third, which has curved hooks on the basal segments in *B. amphitrite*, *B. venustus niveus*, *B. v. obscurus* and to a lesser extent in *B. v. modestus*, these seem to be lacking in *B. venustus* s. str., *B. pallidus pallidus* and *B. pallidus stutsburi*.

The basal segments of the third cirrus of *B. pallidus pallidus* and *B. p. stutsburi* are short and broad and rather hairy compared with the others.

KEY TO DARWIN'S " VARIETIES "

1. Labrum with numerous teeth running down central notch. Shells with longitudinal purple-coloured stripes. Tergum with short spur and more than half its length distant from the basi-scutal angle . . . . ***Balanus amphitrite***
Labrum with few teeth, usually none inside the groove 2

2. Spur two or more times as long as broad. Scutum with triangular dark patch. Parietal walls with supplementary small pores outside the main pores **Balanus pallidus** 3
   Tergum with short spur 4
3. Shell white except for occasionally a pink edge to the compartments **Balanus pallidus** s. str.
   Lower portion of shell purple upper part white . . **Balanus pallidus stutsburi**
4. Tergum with spur less than half its length distant from the basi-scutal angle **Balanus venustus** 6
   Tergum with a tapering spur over half its length distant from the basi-scutal angle. Shell with freckled stripes . . . . . . **Balanus variegatus** 5
5. Scuta with lines of growth not beaded . . . . . . **Balanus variegatus** s. str.
   Scuta with beaded lines of growth (*fide* Darwin) . . **Balanus variegatus cirratus**
6. Upper part of shell white, lower part uniform bluish-grey or with bluish-grey stripes corresponding with the pores in the wall of the shell . **Balanus venustus modestus**
   Shell with coloured or hyaline stripes corresponding with the septa between the pores 7
7. Stripes hyaline white . . . . **Balanus venustus niveus**
   Stripes coloured 8
8. Stripes purplish pink . . . . **Balanus venustus venustus**
   Stripes narrow dark-grey more numerous near the base than higher up, parietal pores subdivided near to base . . . . . . **Balanus venustus obscurus**

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REFERENCES

Broch, H. 1927. Zoological results of the Cambridge Expedition to the Suez Canal, 1924. VII. Report on the Crustacea Cirripedia. *Tr. zool. Soc. Lond.* **22** : 133–137.

Darwin, C. 1854. A monograph on the sub-class Cirripedia. The Balanidae, etc. xi + 400 pp., 31 pls. Ray Society, London.

Pilsbry, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum ; including a monograph of the American species. *Bull. U.S. nat. Mus.* **93** : xi + 366 pp., 76 pls., 99 text-figs.

Pulteney, R. 1799. Catalogues of the birds, shells and some of the more rare plants of Dorsetshire. 92 pp., portr.

Read, R. 1960. Interlaminate figures of sessile barnacle shells. *Nature*, **185** : 778.

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PLATE 1

Balanus amphitrite amphitrite

a, b. The lectotype photographed from the side and from above before dissection.

c, d. Internal and external aspects of the scutum of the lectotype.

e, f. Internal and external aspects of the tergum of the lectotype.

g. The middle portion of the piece of bamboo covered with barnacles and with " *Balanus amphitrite* " in Darwin's handwriting. The specimen selected as the lectotype is the one to the right of the letter " e " in *amphitrite*.

h. A section of one of the parietes of a paralectotype from the bamboo, ground parallel to the basis and lit by glancing surface illumination.

Note: All photographs are by the author. The official photographers have been very cooperative but are in no way responsible for the short comings.

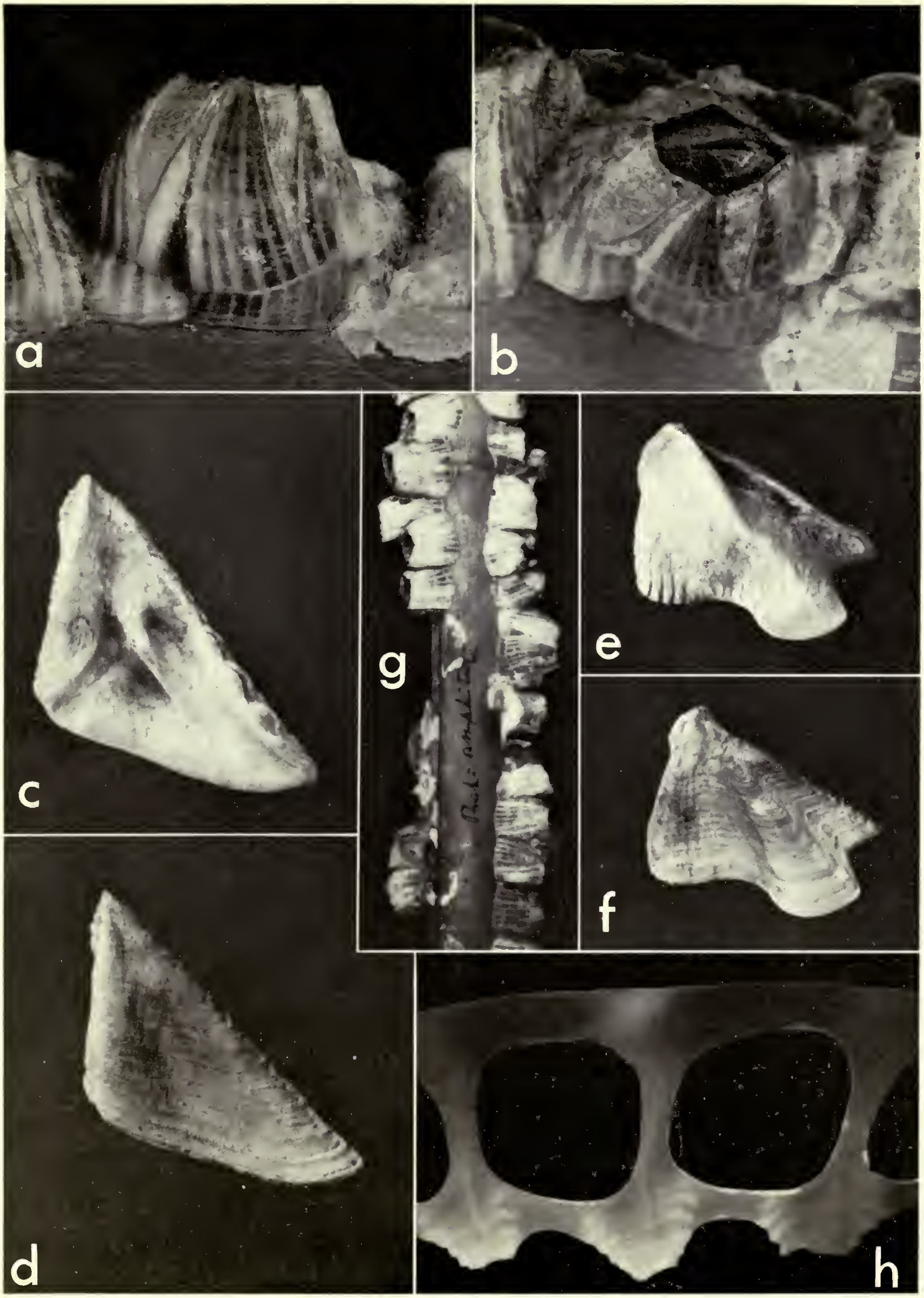
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PLATE 2

Balanus amphitrite amphitrite

Animal parts of the lectotype :

a. Labrum.
b–g. Cirri i–vi in order.
h. Basal segment of Cirrus iii more highly magnified.
j. Mandible.
k. Maxilla.

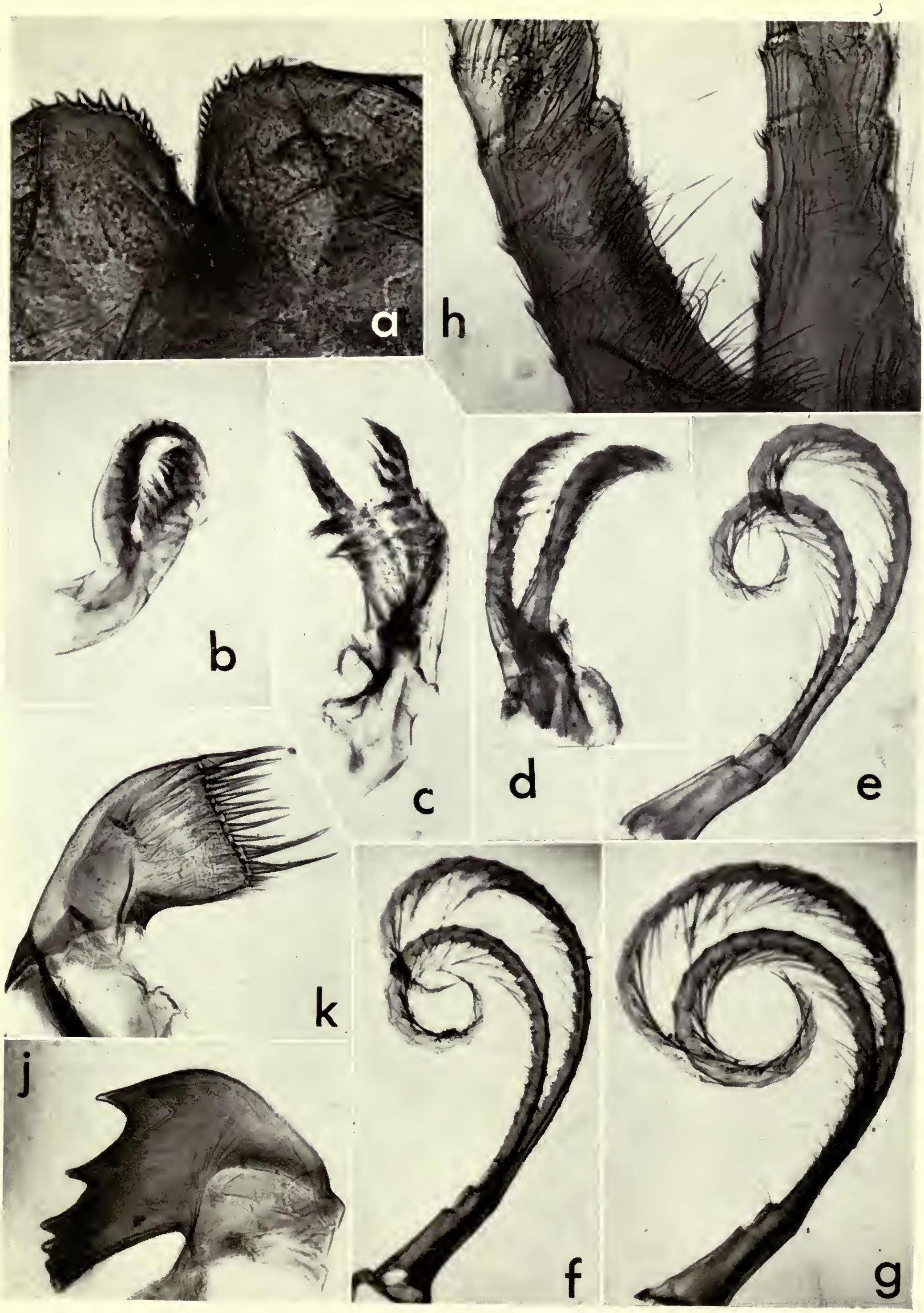
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PLATE 3

Balanus pallidus pallidus

a–d. Various aspects of the lectotype before dissection.
e, f. Internal and external aspects of the tergum of lectotype.
g, h. Internal and external aspects of the scutum of lectotype.
j, k, l. Labrum, mandible and maxilla of lectotype.
m. Section of parietal wall of a paralectotype.
n, o, p, q. Cirri i, ii, iii, iv of lectotype.
r. Basal segments of Cirrus iii of lectotype.

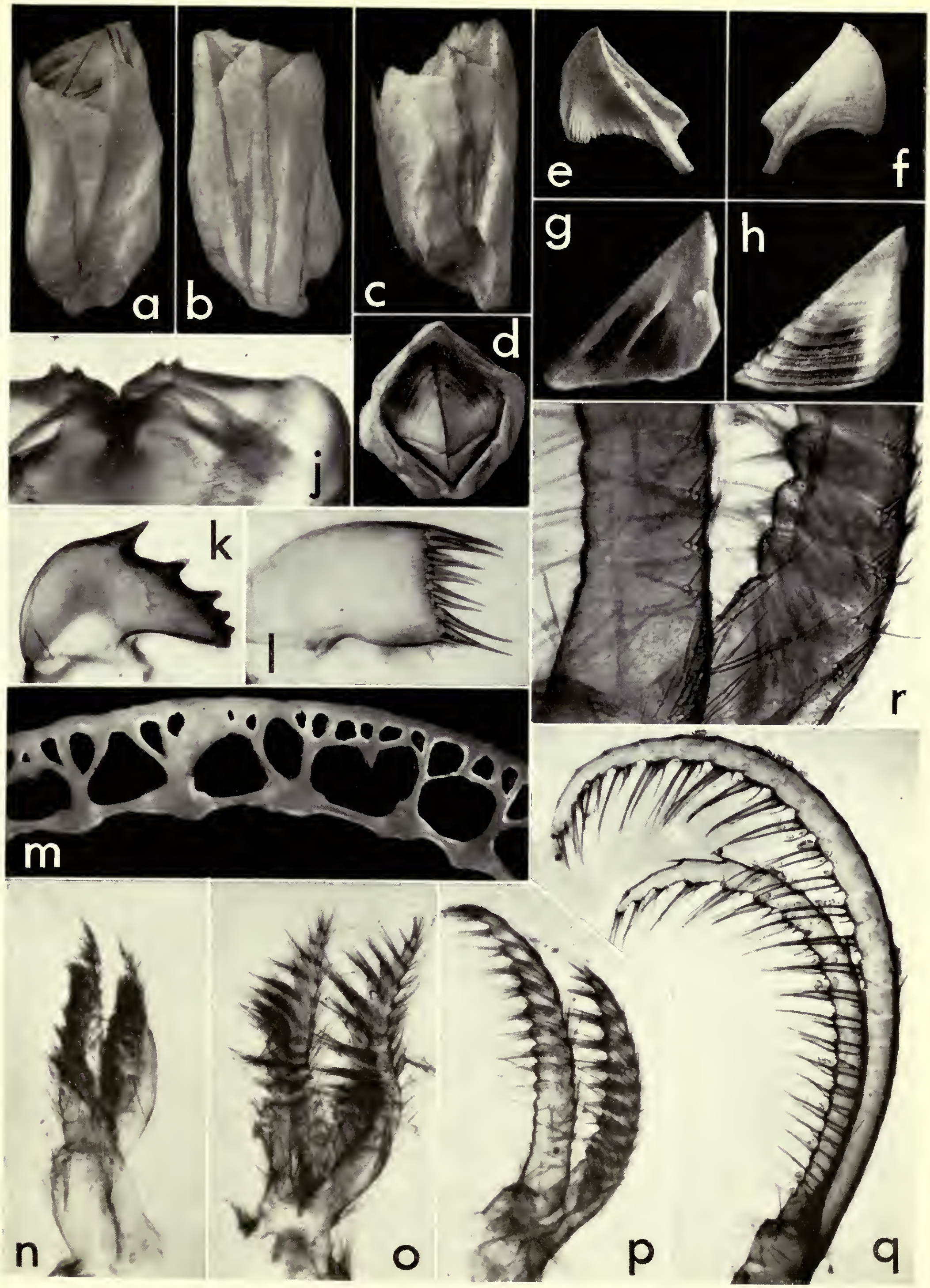
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PLATE 4

Balanus pallidus stutsburi

a, b. Two aspects of Specimen A before dissection.
c, d. Internal and external aspects of scutum of Specimen A.
e, f. External and internal aspects of tergum of Specimen A.
g, h. Sections of parietal walls of another specimen.

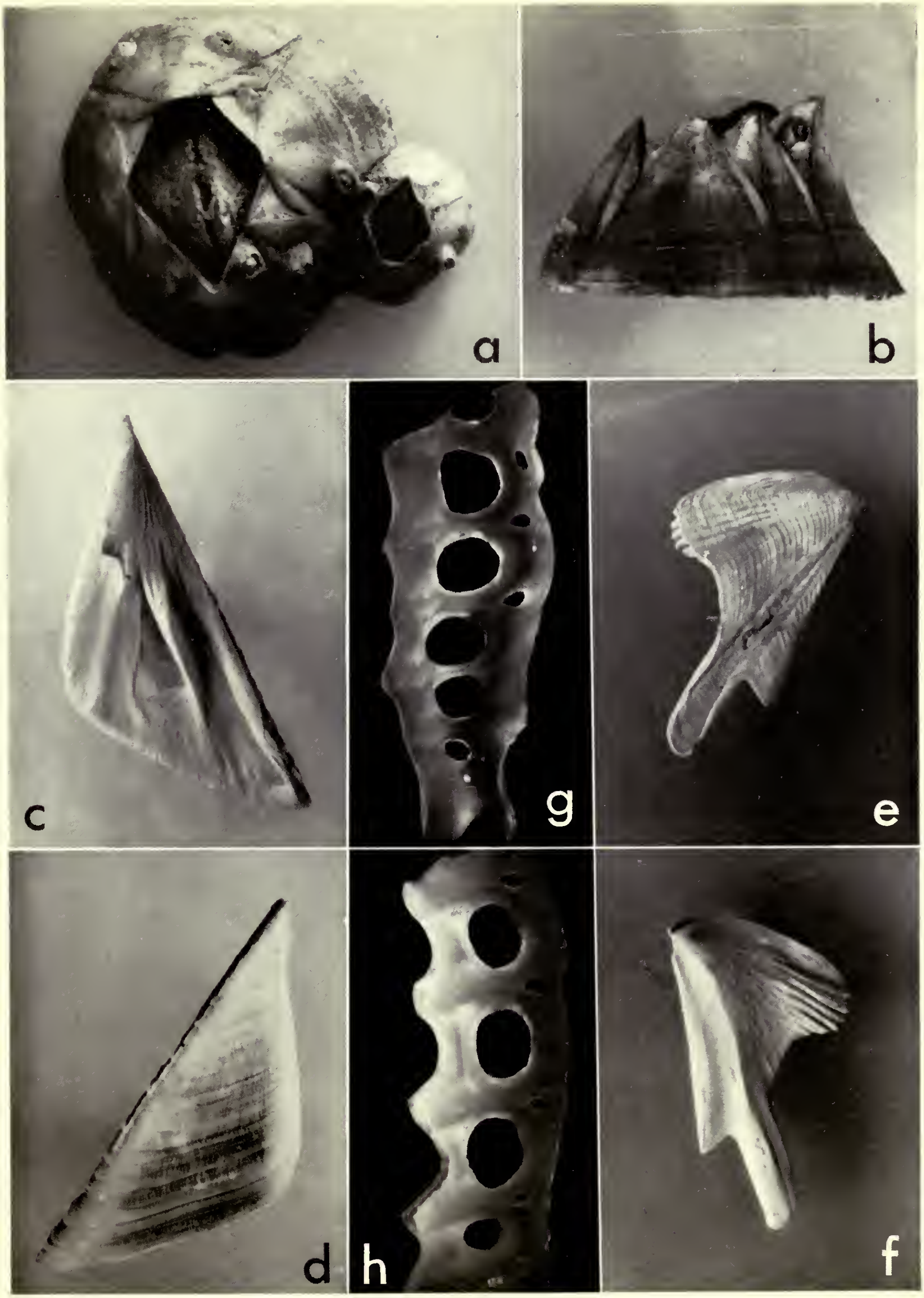
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PLATE 5

Balanus pallidus stutsburi

a. Labrum of Specimen A.
b. Labrum of specimen dissected by Darwin, now in Cambridge.
c. Maxilla of Specimen A.
d. Maxilla of Darwin's dissection, now in Cambridge.
e. Mandible of Specimen A.
f, g, h, i. Cirri i, ii, iii, iv of Specimen A.
k. Basal segments of Cirrus iii of Specimen A.

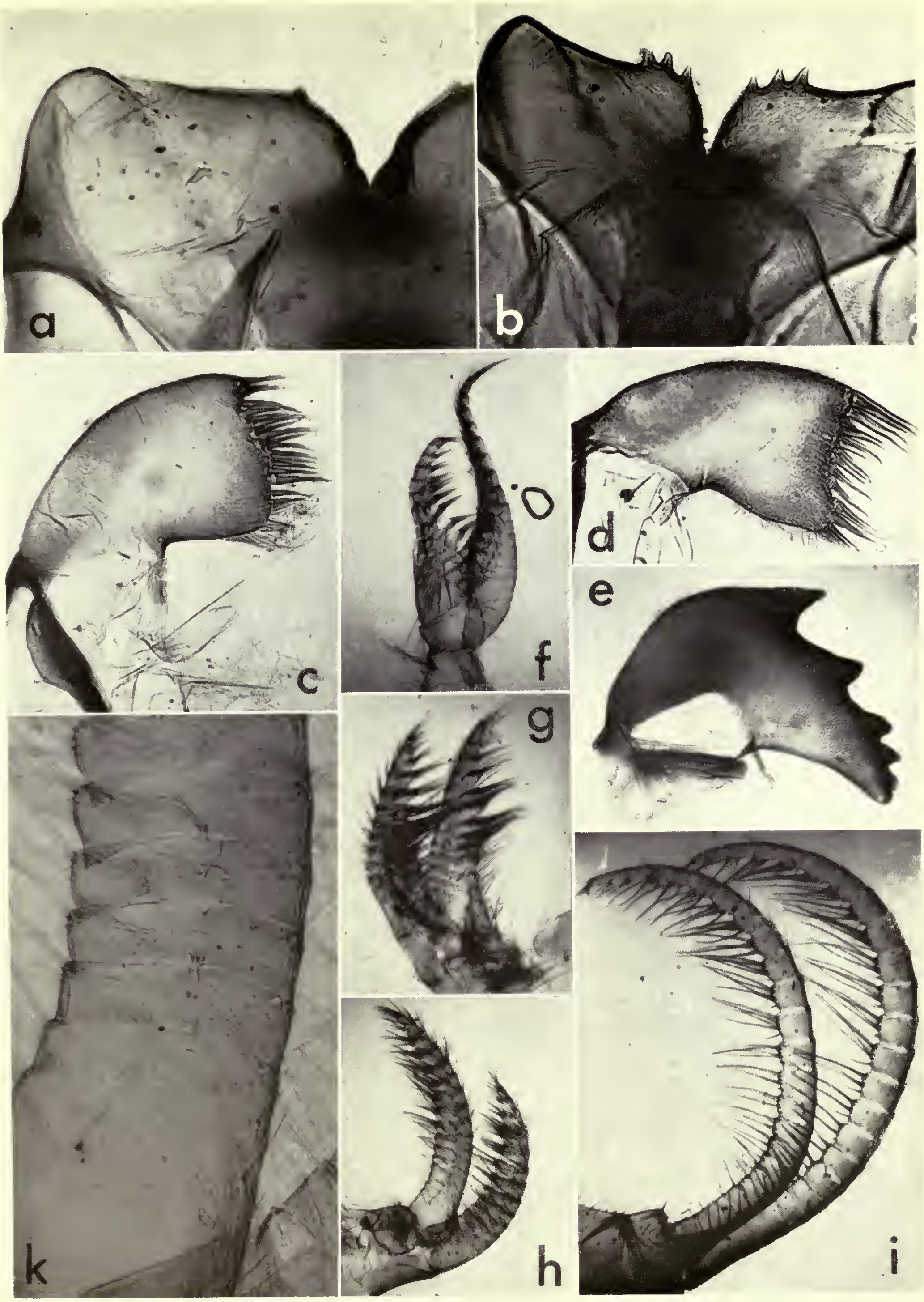
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PLATE 6

Balanus venustus venustus

a, b. Two aspects of the lectotype before dissection.
c. Labrum.
d, e. Internal and external aspects of the scutum.
f, g. Internal and external aspects of the tergum.
h. Section of parietal wall of a paralectotype.
j, k, l. Cirri i, ii, iii.
m. Cirrus v.
n. Mandible.
o. Maxilla.
p. Basal segments of Cirrus iii.

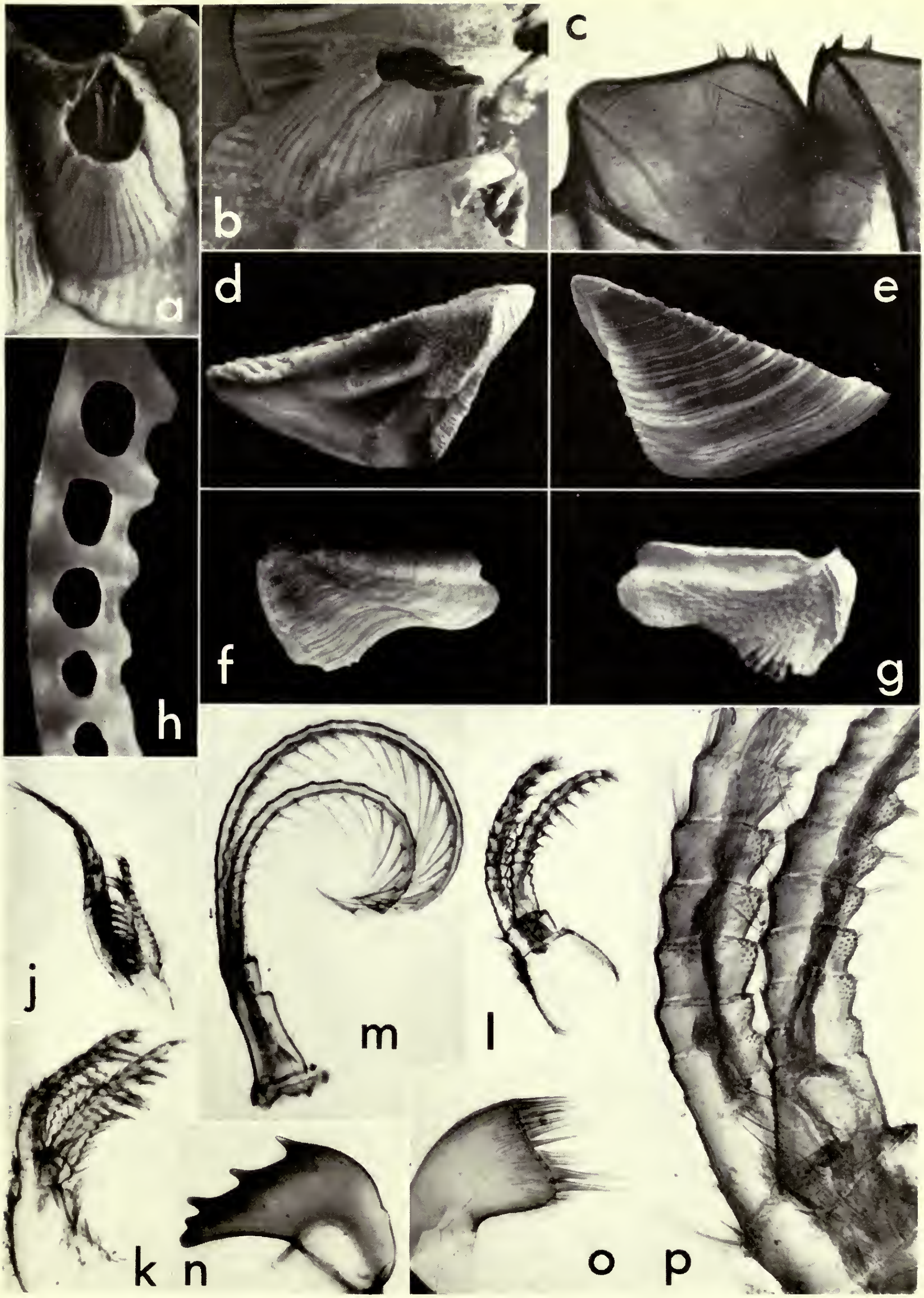
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PLATE 7

Balanus venustus niveus

a, b. Two aspects of the lectotype, the remains of the soft parts can still be seen although the opercular valves have been taken out.

c. " Shell 32." The specimen figured in Darwin's Monograph (pl. 5, 2, *f*).

d, e. External and internal aspects of the tergum of the lectotype.

f, g. Internal and external aspects of the scutum of the lectotype.

h. Mandible of the lectotype.

j, k. Section of bases of parietes of another specimen from the same slab as the lectotype.

l. Labrum of lectotype.

m. Maxilla of lectotype.

n, o, p. Cirrus i, ii, iii of lectotype.

q. Cirrus vi of lectotype.

r. Basal segments of Cirrus iii of lectotype.

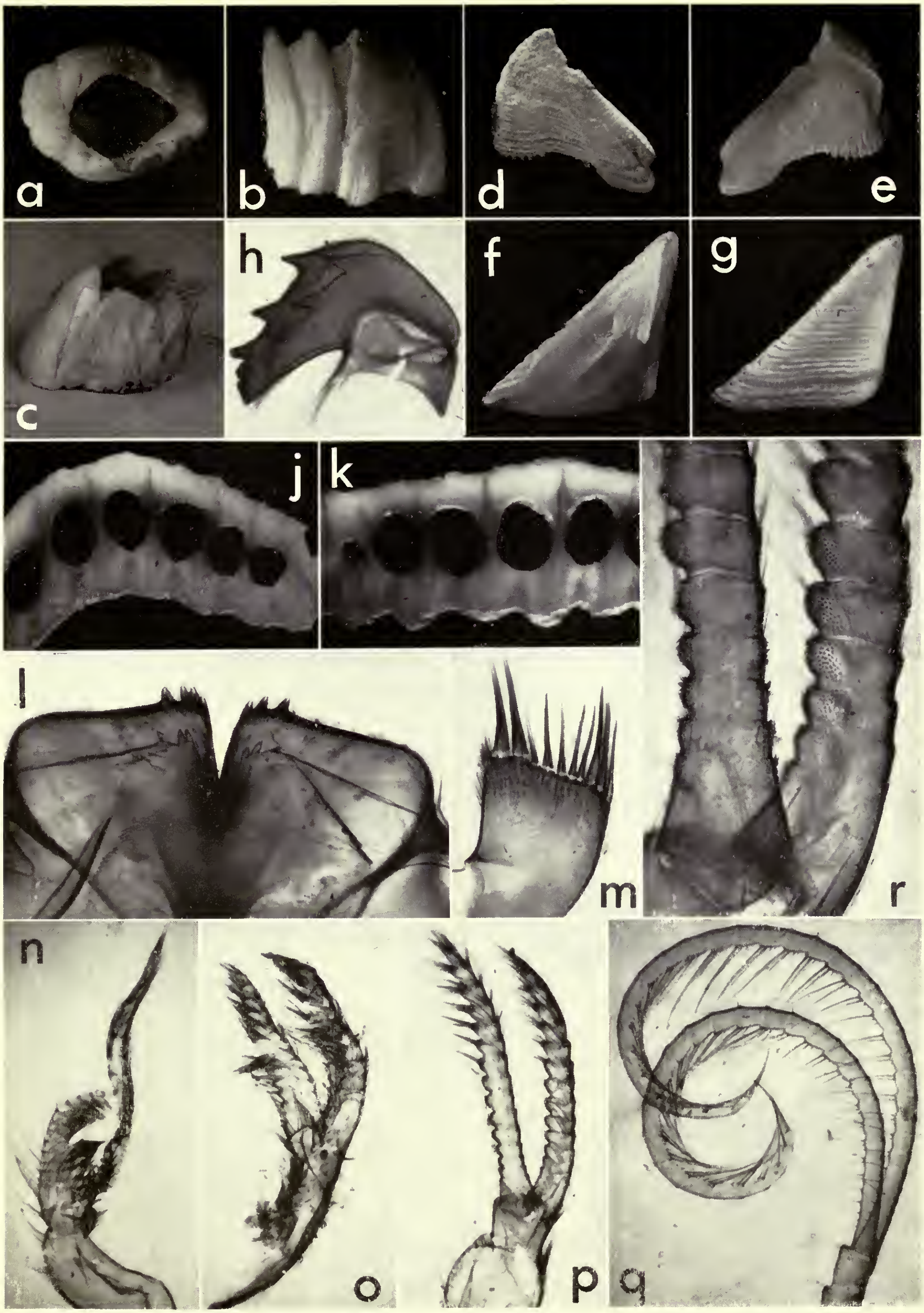
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PLATE 8

Balanus venustus modestus

a, b. Two aspects of a group on a mollusc shell. The specimen with opercular valves is the lectotype. These were photographed before dissection.

c. Section of a parietal wall of one of the paralectotypes.

d, e. External and internal aspects of the scutum of the lectotype.

f, g. External and internal aspects of the tergum of the lectotype.

h, j. Mandible of maxilla of lectotype.

k, l, m. Cirri i, ii, iii of the lectotype.

n. Cirrus v of the lectotype.

o. Basal segments of Cirrus iii of lectotype.

p. Labrum of the lectotype.

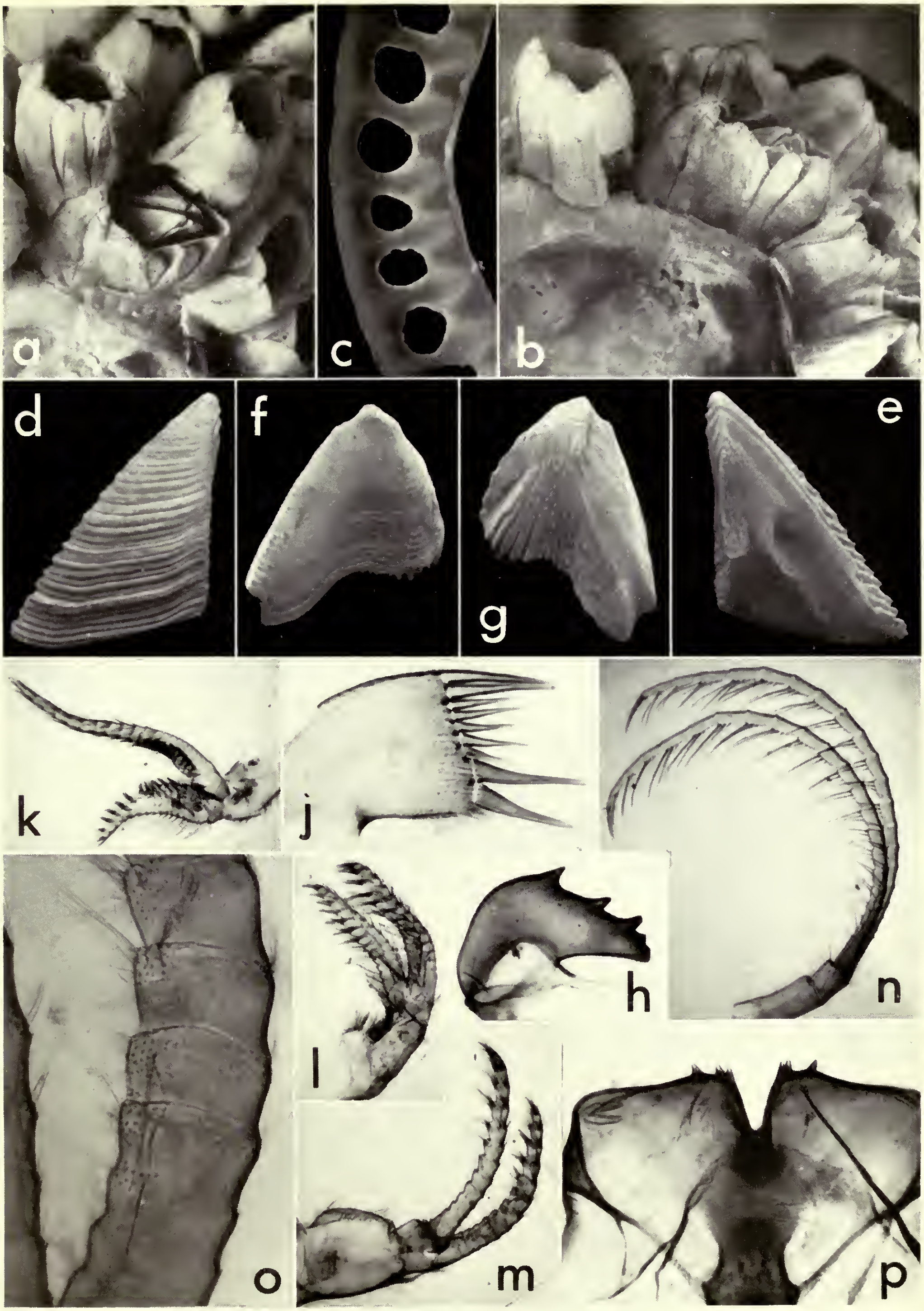
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PLATE 9

Balanus venustus obscurus

a, b. Two aspects of the lectotype before dissection.
c, d External and internal aspects of the scutum of the lectotype.
e,f . External and internal aspects of the tergum of the lectotype.
g, h, j. Cirri i, ii, iii of the lectotype.
k. Cirrus vi of the lectotype.
l, m, n. Maxilla, mandible and labrum of the lectotype.
o, p. Sections of parietal walls of a paralectotype.
q. Basal segments of Cirrus iii of lectotype.

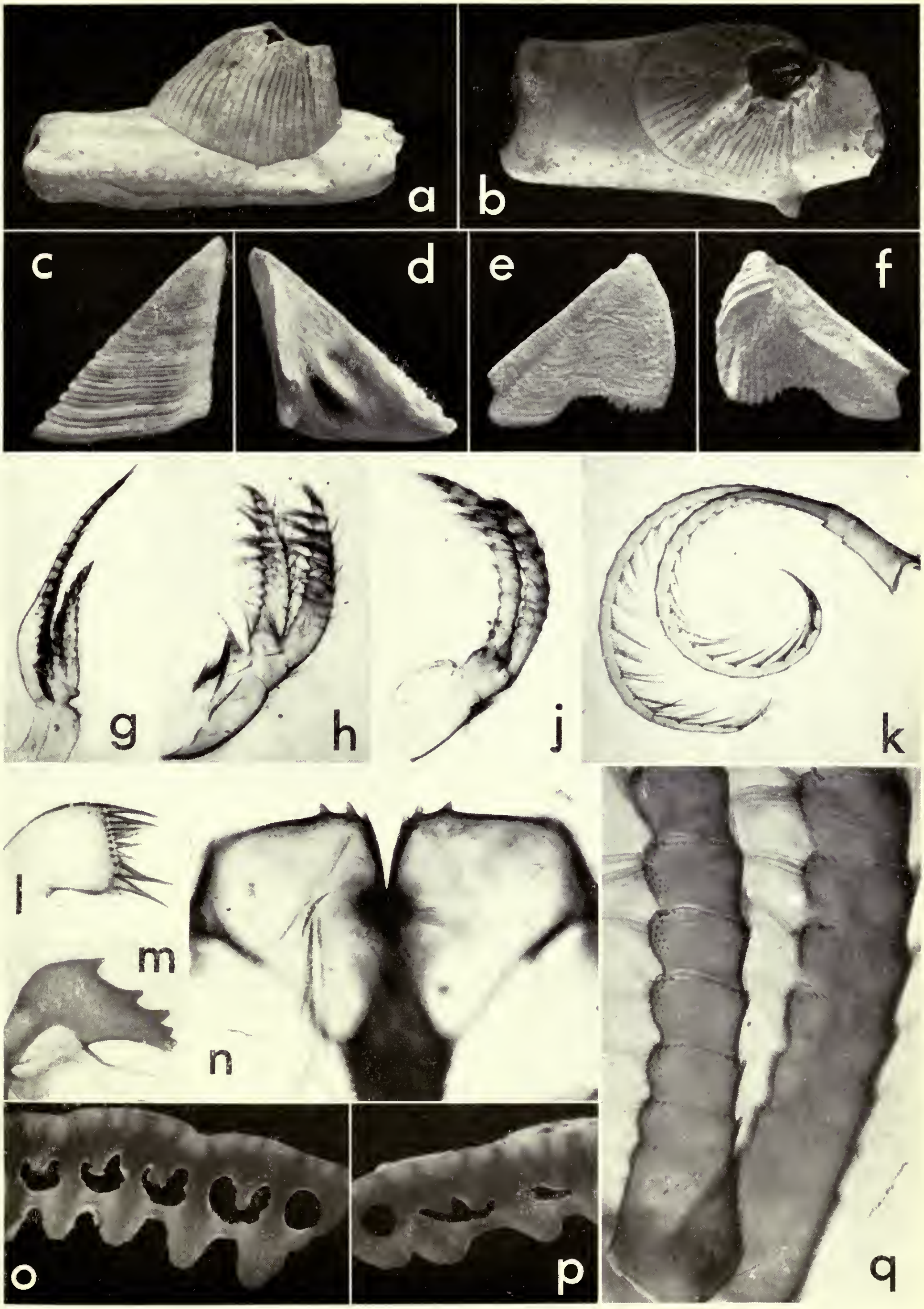
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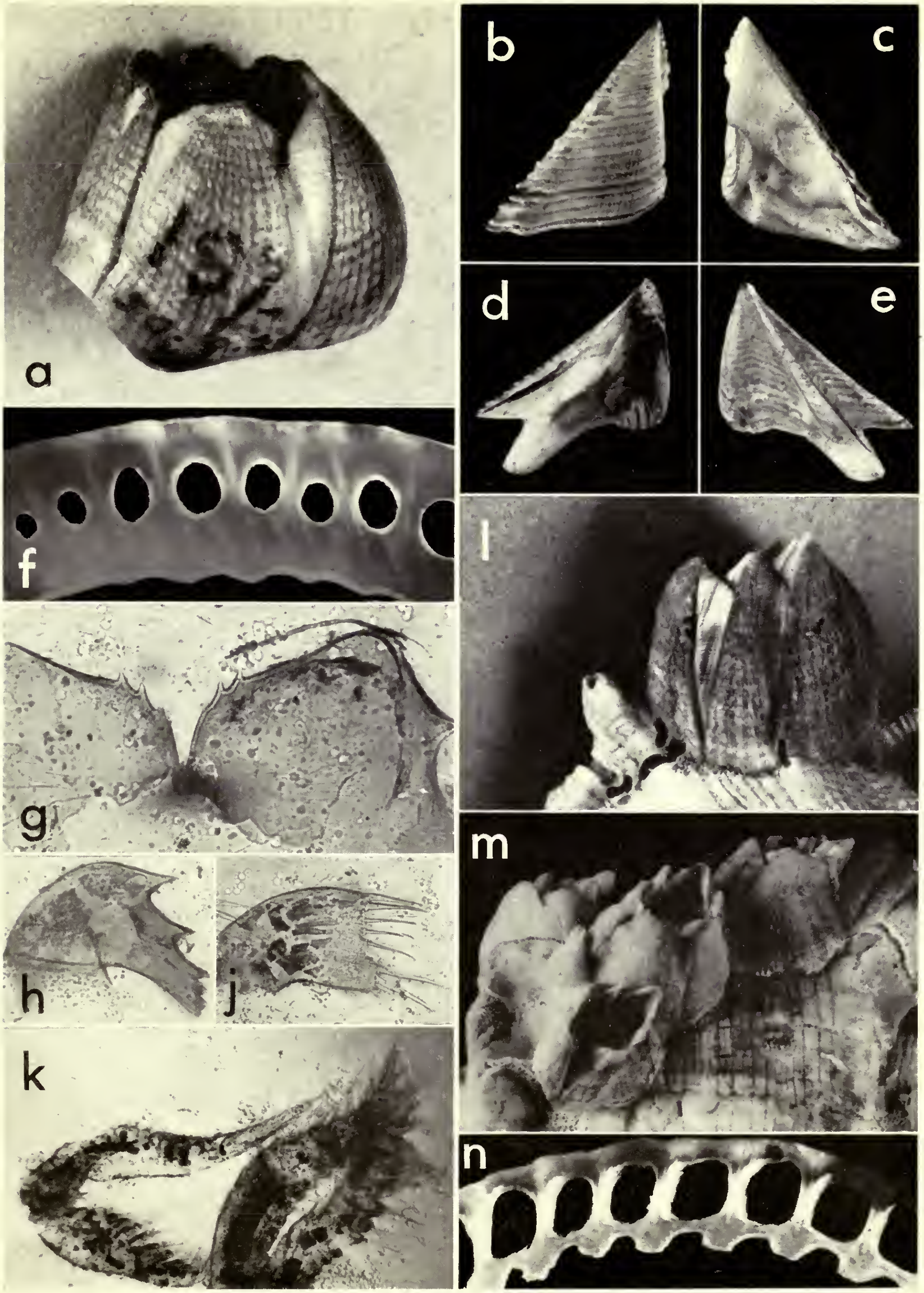
PLATE 10

a–k. Balanus variegatus variegatus

a. Lectotype.
b, c. External and internal aspects of the scutum of lectotype.
d, e. Internal and external aspects of the tergum of the lectotype.
f. Section of parietal wall of lectotype.
g, h, j. Labrum, mandible and maxilla of the Cambridge paralectotype.
k. Cirri i, ii of the Cambridge paralectotype.

l–n. Balanus variegatus var. *cirratus*

l. Large specimen from Slab 16.
m. A group of specimens on Slab 35.
n. A section of parietal wall of a specimen from Slab 35.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A REVISION OF THE GENUS *GORDIODRILUS* BEDDARD (OLIGOCHAETA : MEGASCOLECIDAE)

BRITISH MUSEUM
14 MAY 1963
NATURAL HISTORY

BARRIE G. M. JAMIESON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 9 No. 8
LONDON: 1963

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BY

BARRIE G. M. JAMIESON

(University of Sydney)

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A REVISION OF THE GENUS *GORDIODRILUS* BEDDARD (OLIGOCHAETA: MEGASCOLECIDAE)

By B. G. M. JAMIESON

SYNOPSIS

Nannodrilus Beddard, 1894, and *Diaphorodrilus* Cognetti, 1910, are removed from the synonymy of *Gordiodrilus* Beddard, 1892, and *G. luykerleni* Michaelsen, 1913, and *G. overlaeti* Michaelsen, 1936, are transferred to the genus *Ilyogenia* Beddard. The restricted *Gordiodrilus* is divided into five species-groups: an *elegans* group of fifteen species and four monotypic groups, a *tenuis* group, a *robustus* group, a *pampaninii* group and a *papillatus* group.

The phylogeny of *Nannodrilus* and *Gordiodrilus* is discussed and it is suggested that the *Notiodrilus* ancestor of classical theory should be replaced by a sexprostatic form similar to that postulated by Gates (1942). Some evidence is presented for regarding an even more extensive series of prostates as the primitive condition in the Ocnerodrilinae (and perhaps the Megascolecidae as a whole).

Keys and definitions of the species-groups and species of the restricted *Gordiodrilus* are given.

INTRODUCTION

"I CAN do nothing with this heterogeneous group", so wrote Stephenson (1930) of *Gordiodrilus* Beddard, 1892. The genus had already seemed heterogeneous to Beddard when he reviewed it in 1895. Beddard was of the opinion that *G. tenuis* Beddard, 1892, showed some claims to being regarded as a separate genus, that *G. robustus* Beddard, 1892, stood alone, linking *Gordiodrilus* with *Ocnerodrilus* Eisen, and that the four remaining species, *G. elegans* Beddard, 1892, *G. ditheca* Beddard, 1892, *G. dominicensis* Beddard, 1892, and *G. zanzibaricus* Beddard, 1894*a*, formed a distinct group.

In 1913 Michaelsen included *Nannodrilus* (then containing *N. africanus* Beddard, 1894*b*, *N. phreoryctes* Michaelsen, 1903, and *N. staudei* Michaelsen, 1897) with *Diaphorodrilus* (a monotypic genus established for *D. doriae* Cognetti, 1910) in *Gordiodrilus* because he considered that the male and prostatic terminalia of *Gordiodrilus elegans*, *G. luykerleni* Michaelsen, 1913, *Nannodrilus staudei*, *N. africanus* and *G. togoensis* Michaelsen, 1913 formed a continuous series. (He preceded the series with *Eukerria* which, however, he did not unite with *Gordiodrilus*.) Chiefly as a result of uniting the, in part, sexprostatic *Nannodrilus* with the previously quadriprostatic *Gordiodrilus*, Michaelsen included *Diaphorodrilus* which has three pairs of prostates.

Stephenson (1930) believed *Gordiodrilus* to be evolving along various lines and to be raw material from which many distinct genera were still to be produced.

His diagnosis of *Gordiodrilus* (s. Mich.), which he admitted to be meaningless, is as follows :—

" Condition of male apparatus very various—incompletely or irregularly microscolecine, or showing a tendency to balantine reduction, or megascolecine. Two or one or no gizzards. A single oesophageal sac, or a pair, in ix. Holandric, metandric, or proandric (*G. chuni*). Spermathecae without diverticula on the duct, but sometimes with evaginations at the ectal end of the ampulla."

Twenty species were known when this was written and nine have since been described.

Gates (1942) described *Gordiodrilus* as " one of the most difficult problems in Megadrilid taxonomy " and (1957) a " taxonomic waste-basket ". He divided the genus into " generic groups " (Table I) for which he gave definitions (1942). His examination of material was limited, however, to *Gordiodrilus peguanus* Gates, 1942, and he stated that it should not be considered that he had restricted the genus.

TABLE I.—*Gates' (1942) Analysis of Gordiodrilus*

Gordiodrilus (S. Mich.)

- TENUIS DIVISION
  - UNICUS GROUP
    - *unicus*
  - ZANZIBARICUS GROUP
    - *zanziburicus*
    - *habessinus*
    - *paski*
    - *wemanus*
    - *peguanus*
    - Possibly also :
      - *dominicensis*
      - *chuni*
  - TRAVANCORENSIS GROUP
    - *travancorensis*
    - *madagascariensis*
    - *elegans*
    - Possibly also :
      - *mobucanus*
  - PAPILLATUS GROUP
    - *papillatus*
  - TENUIS GROUP
    - *tenuis*
  - DITHECA GROUP
    - *ditheca*
- NANNODRILUS DIVISION
  - *africanus*
  - *staudei*
  - *phreoryctes*
  - *schubotzi*
  - Perhaps also :
    - *togoensis*
    - *johneni*
- ROBUSTUS DIVISION
  - *robustus*
  - *congicus*
  - *pampaninii*
- DIAPHORODRILUS DIVISION
  - *doriae*
  - *luykerleni*
  - *thomseni*
  - *overlaeti*

Perhaps the most important aspect of this valuable paper was the suggestion (pp. 78, 80) that *Gordiodrilus* could be derived from sexprostatic forms. This released Megascolecid taxonomy from the restrictions of the orthodox theory of origin from the quadriprostatic acanthodriline *Notiodrilus* ancestor (see Phylogenetic Considerations, below).

The present review originated during a study of material of the Ocnerodrilinae. As the study progressed it became possible to suggest a solution to the problem of the classification of the genus. The new classification and the reasons for it are presented in this work.

MATERIAL AND ACKNOWLEDGMENTS

This work was made possible by grants from the Goldsmiths' Company of London and the Department of Scientific and Industrial Research.

The paper is based on part of a section on the Ocnerodrilinae in a doctorate thesis submitted to the University of Bristol in 1958. I am indebted to Professor J. E. Harris of Zoology Department, University of Bristol, Professor L. C. Beadle of Zoology Department, Makerere College, Uganda, and the Trustees of the British Museum (Natural History) for the facilities which they put at my disposal in these institutions and to Professor K. von Haffner for permitting me to examine material in the collections of the Zoological Museum, Hamburg. My special thanks are due to Dr. R. B. Clark of Zoology Department, University of Bristol, for his advice and helpful criticism throughout the progress of the work, and I also thank Mr. R. W. Sims, Mr. N. Tebble and Miss Angela Edwards of the British Museum (Natural History) for their valuable assistance. I am also grateful to members of the Museum staff, and to Dr. D. T. Anderson of Zoology Department, University of Sydney, for their critical appraisal of the manuscript.

SYSTEMATICS

Before discussing the genus *Gordiodrilus* in the sense which it is restricted here, the taxa which are removed and the reasons for their exclusion will be given.

EXCLUSION OF *Nannodrilus*. Michaelsen's series (see above) for the union of *Nannodrilus* and *Gordiodrilus* arose largely from consideration of the morphology of *G. luykerleni* Michaelsen, 1913. The series shows defects which, in my opinion, invalidate union of the two genera.

First, *G. luykerleni*, in which one pair of prostatic ducts discharges in common with the thickened male ducts, is seen by its male terminalia and paired oesophageal diverticula, in addition to complete somatic identity, to be an *Ilyogenia*. Michaelsen considered it to link those species of *Gordiodrilus* (s. Beddard) in which the ducts discharge separately and are unthickened (e.g. *G. elegans*) with *Nannodrilus* in which at least one pair of prostatic ducts always discharges in common with the constantly thickened male ducts.

Secondly, a survey of the six species here included in *Nannodrilus* suggests, as Gates (1942) has proposed, that *Nannodrilus* is basically sexprostatic (see pp. 320–321 below). Derivation of a sexprostatic *Nannodrilus* from an acanthodrilin quadriprostatic *Eukerria* is improbable and does not easily allow the construction of a series of the type which Michaelsen has advanced for the union of *Gordiodrilus* and *Nannodrilus*.

A consideration of somatic characters shows Michaelsen's series to be equally inacceptable. The stages in the series : *Eukerria—Gordiodrilus elegans—G. luykerleni* involve reduction of the pair of oesophageal diverticula of *Eukerria* to the single midventral sac of *Gordiodrilus* (s. Beddard) and a reversal of this reduction to give the pair of sacs of *luykerleni*—an unlikely sequence. *Nannodrilus* should, therefore, be reinstated as a separate genus.

Gates' (1942) *Nannodrilus* division was co-ordinate with his *tenuis*, *robustus* and *Diaphorodrilus* divisions, each of which was virtually a genus and was given a " generic " definition although he did not designate them genera. He excluded *G. togoensis* Michaelsen, 1913, and *G. johneni* Michaelsen, 1936, from the division because they lack gizzards. I do not consider this to invalidate their inclusion in *Nannodrilus* (Jamieson, 1962*b*, footnote p. 619) and have transferred them from *Gordiodrilus* to this genus.

Exclusion of *Diaphorodrilus*. Gates regarded the species in his *Diaphorodrilus* division (*G. doriae* (Cognetti, 1910), *G. overlaeti* Michaelsen, 1936, *G. luykerleni luykerleni* Michaelsen, 1913, and *G. luykerleni thomseni* Michaelsen, 1933, the latter regarded by Gates as specifically distinct) as having little in common, and was able to give only a brief diagnosis. The only feature which he could find to diagnose the group from all other Ocnerodrilinae was a constant segmental location of the spermathecal pores. As I have found these pores to be intersegmental in one apparently normal specimen of *luykerleni*, the character appears to be unreliable.

I propose that *overlaeti*, like *luykerleni*, should be transferred to *Ilyogenia*,[1] leaving only *doriae* in the *Diaphorodrilus* division. The sexprostatic *doriae* has a pair of oesophageal diverticula and has little in common with the quadriprostatic, unicaecal *Gordiodrilus*. I therefore propose to reinstate the genus *Diaphorodrilus* Cognetti, 1910, of which *doriae* is the type and sole species.

The restricted *Gordiodrillus*

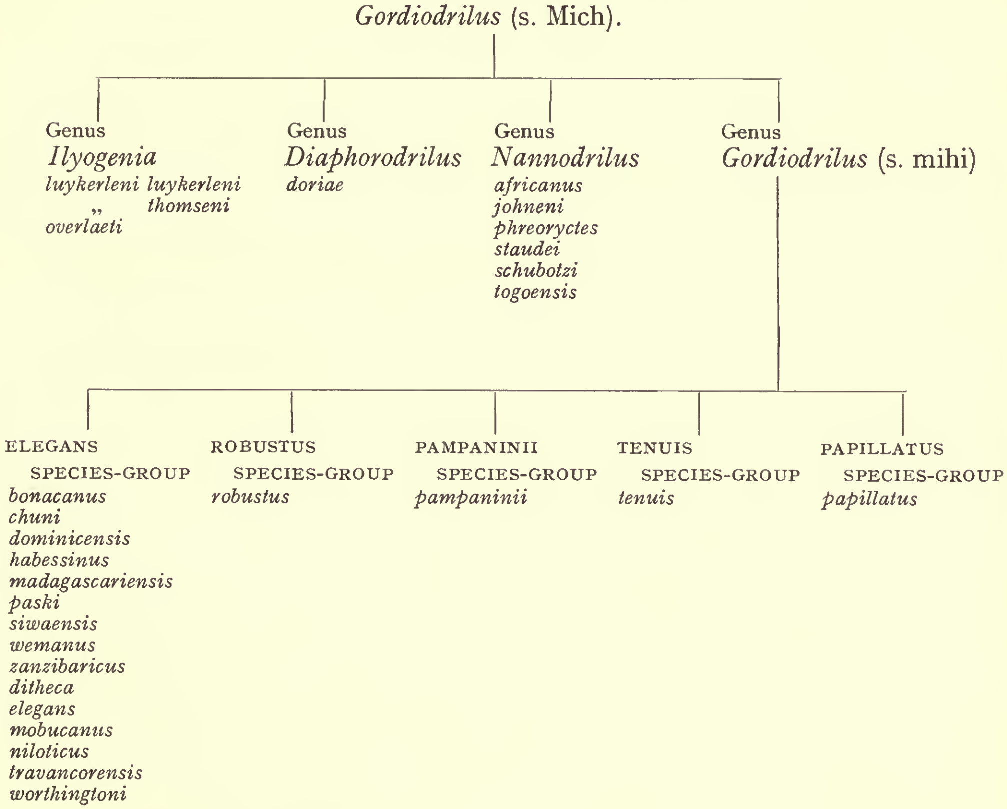
The restriction of *Gordiodrilus* (s. Mich.) proposed above (see also Table II) leaves only Gates' *tenuis* division (divided by Gates into six groups, Table I) and his *robustus* division (containing *G. robustus*, *G. pampaninii* and *congicus*) to be considered. The species they contain constitute *Gordiodrilus* (s. mihi) which is here divided into five species-groups : an *elegans* group of fifteen species and four monotypic species-groups, a *tenuis* group, a *robustus* group, a *pampaninii* group and a *papillatus* group. The grounds for recognizing these species-groups are best shown by a discussion of Gates' two divisions.

The species of Gates' *tenuis* division (Table I) share with his *robustus* division a quadriprostatic condition, with the prostatic pores at the termini of the seminal grooves in which lie the male pores in an intermediate position, but differ in lacking a gizzard. Gates stated that *G. tenuis* should be regarded as a specialized representative of the species placed in the *tenuis* division because it maintains the gordiodrilin approximation to an acanthodrilin condition of the male terminalia. Its affinities with these species seem doubtful and I share with Beddard (1895) the view that *tenuis* has some claims to being regarded as generically distinct. Peculiar features of *G. tenuis* are the far posterior position of its male and prostatic pores (xx to xxi), the great length of the clitellum (xiv to xxvii) and the possible metandry. The extraordinary length of the clitellum seems not to be explicable merely by its having been drawn out in response to backward movement of the prostatic and male pores for, in *G. papillatus*, where the pores are in xix and xx, the anterior limit of the clitellum is xviii. For the present *tenuis* becomes the sole representative of a *tenuis* species-group within the restricted *Gordiodrilus*.

---

[1] *Ilyogenia luykerleni* (Mich.) is intermediate between most species of *Ilyogenia*, which have the male and prostatic pores on xvii (with, in one case, *I. limicola*, a further pair of prostatic pores on xviii) and *I. chubbi* and *I. overlaeti* (Mich.) which have male and prostatic pores on xix with a further pair of prostatic pores on xx. *I. luykerleni* has pores on xviii (and additional prostatic pores on xix in *I. l. luykerleni*). It is the only member of *Ilyogenia* with two pairs of spermathecae. That *I. overlaeti* is distinct from *I. chubbi* is very doubtful.

TABLE II.—*Present Analysis of Gordiodrilus*



Gordiodrilus (s. Mich).

- Genus *Ilyogenia*
  - *luykerleni luykerleni*
  - ,, *thomseni*
  - *overlaeti*
- Genus *Diaphorodrilus*
  - *doriae*
- Genus *Nannodrilus*
  - *africanus*
  - *johneni*
  - *phreoryctes*
  - *staudei*
  - *schubotzi*
  - *togoensis*
- Genus *Gordiodrilus* (s. mihi)
  - ELEGANS SPECIES-GROUP
    - *bonacanus*
    - *chuni*
    - *dominicensis*
    - *habessinus*
    - *madagascariensis*
    - *paski*
    - *siwaensis*
    - *wemanus*
    - *zanzibaricus*
    - *ditheca*
    - *elegans*
    - *mobucanus*
    - *niloticus*
    - *travancorensis*
    - *worthingtoni*
  - ROBUSTUS SPECIES-GROUP
    - *robustus*
  - PAMPANINII SPECIES-GROUP
    - *pampaninii*
  - TENUIS SPECIES-GROUP
    - *tenuis*
  - PAPILLATUS SPECIES-GROUP
    - *papillatus*

The remaining groups into which Gates split his *tenuis* division may now be considered. The *unicus* group is no longer valid as *unicus* has been synonymized with *paski* (see Jamieson, 1962*a*). The *zanzibaricus* group (prostates in xvii and

xviii) and the *travancorensis* group (prostates in xviii and xix) are here united as the *elegans* group. Although their separation probably has some phylogenetic basis (see p. 321), it seems possible that in some cases the variation in location of the pores occurs intraspecifically. Thus the separation of *G. bonacanus* Cernosvitov, 1942, with prostates in xvii and xviii, and *G. travancorensis* Michaelsen, 1910, with prostates in xviii and xix, is questionable (Jamieson, 1962*c*; both occur outside Africa and may be peregrine forms of the same species). A similar variation occurs intraspecifically in *Ilyogenia christyi* Stephenson, 1928.

Of the species which Gates considered to belong only doubtfully to his *tenuis* division, i.e. *G. ditheca*, *dominicensis*, *mobucanus*, *chuni* and *papillatus*, the first four appear to be members of the *elegans* species-group. *G. ditheca* is probably a variant of *G. elegans*, as Michaelsen (1933) believed; *G. dominicensis* need not be excluded because it is athecal; *G. mobucanus* is a normal member of the group except in the reported post-setal location of its female pores, an observation requiring confirmation; *G. chuni* is referable to the group, its bithecal condition appearing to be an expected reduction, but the extraordinary length and attenuation of the spermathecal ducts, seen elsewhere only in *robustus*, *tenuis* and *papillatus*, may indicate that it should be separated.

I follow Gates in referring *G. papillatus* to a distinct, monotypic group. The combination of characters which distinguishes *papillatus* from other members of the restricted *Gordiodrilus* is: the far posterior position of the male genital field (prostatic pores in xix and xx), the presence of genital markings, the setal disparity and, most important, the presence of bursae copulatrices. Gates recognized the distinct position of *papillatus* and mentioned that there is a remote possibility that it provides a transition between his *travancorensis* group and *tenuis* group; alternatively, he stated that if gizzards and prostates opening into the bursae copulatrices had been overlooked, *papillatus* could be included in *Nannodrilus*. I have suggested (p. 302 and 1962*b*) that the absence of gizzards need not exclude a species from *Nannodrilus*; nevertheless, the absence of prostates opening into the bursae taken with the intersegmental position of the male pores and the presence of seminal grooves does seem to exclude *papillatus*. The possible phylogenetic relationships of the species are discussed below under Phylogenetic Considerations.

The main diagnostic characteristics of Gates' " generic " definition of the *robustus* division (i.e. the presence of gizzards, the unusually long spermathecal ducts and the presence of genital markings behind the male genital region) mark off the division from other gordiodrilids. But phylogenetic considerations (p. 321 below) suggest that *robustus* (including *congicus*) and *pampaninii* should each be regarded as typical of a separate group within *Gordiodrilus* (s. mihi).

It seems unnecessary to follow Gates' suggestion that, if Beddard's statement were correct and one specimen of *G. robustus* had paired oesophageal sacs, this species would have to be referred to a distinct genus. Pairing, to a lesser extent, in this species has been reported by Michaelsen (1936) and by myself (1963) and does not seem to be of a type which would give rise to paired sacs of the type seen in genera which normally show pairing. The sacs remain ventral and sessile and retain the appearance of a bifurcated gordiodrilid or nannodrilid sac.

THE NEW CLASSIFICATION

Family MEGASCOLECIDAE

Subfamily OCNERODRILINAE

Genus *GORDIODRILUS* Beddard, 1892

Gordiodrilus Beddard, 1892. *Ann. Mag. nat. Hist.* (6) **10** : 93–94.
Gordiodrilus: Beddard, 1895. A Monograph of the Order Oligochaeta. Oxford. Clarendon Press: 506–507.
Gordiodrilus : Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta : 373.
Gordiodrilus (part.) : Michaelsen, 1913. *Zoologica*. Stuttgart, **68** : 3–5.
Gordiodrilus (part.) : Stephenson, 1930. The Oligochaeta. Oxford : 863.
Gordiodrilus (part.) : Gates, 1942. *Bull. Mus. comp. Zool. Harvard*, **89**, no. 13 : 75–85.
[non] *Nannodrilus* Beddard, 1894*b*. *Proc. zool. Soc. Lond.* **1894** : 388.
[non] *Diaphorodrilus* Cognetti, 1910. *Ann. Mus. civ. nat. Genova*,(3) **4** : 107.

TYPE-SPECIES: *Gordiodrilus elegans* Beddard, 1892[1]. *G. elegans* is here designated the type-species of *Gordiodrilus* because it was the first species to be described in the largest species-group in the genus. Descriptions of *G. tenuis* and *G. robustus* preceded it in Beddard (1892) but each of these is placed in the present work in a monotypic species-group which has claims to being regarded as a genus.

DEFINITION. Fairly small, usually limnic, worms. Number of segments of the order of 100. Prostomium usually epilobous, sometimes pro-epilobous, or zygolobous. Setae lumbricine, closely paired, one or more of each ventral pair often absent in the prostatic segments. Genital, but not penial, setae sometimes developed ; *dd* = 0·4 to 0·5 *u*. Clitellum ring-shaped or saddle-shaped, or a combination of the two, usually extending from a part or the whole of xiii (or xii) to part or the whole of that behind the last prostatic pores, rarely more extensive, the most posterior limit xxvii. Prostatic pores paired in xvii and xviii or less frequently in xviii and xix, rarely in xix and xx or xx and xxi, abnormally (?) in xviii only ; a seminal groove probably always present, connecting the pores of each side. Male pores, one in each seminal groove, in or near the intersegmental furrow between the corresponding prostatic pores. Female pores anterior to the setal zone of xiv, exceptionally near the posterior margin of this segment. Spermathecal pores usually two pairs, one in each of intersegmental furrows 7/8 and 8/9 or rarely 6/7 and 7/8, sometimes one pair behind (or in ?) 7/8 ; sometimes absent.

Septal glands anterior to and including vii or viii. Oesophagus usually without a gizzard ; exceptionally with a well-developed gizzard in vii or with a vestigial gizzard in this segment and a well-developed gizzard in viii ; the oesophagus always bearing midventrally in ix a sessile unpaired or rarely paired[2] oesophageal pouch, which has at most a small lumen, the thick apparently syncytial walls of which are permeated by numerous, perhaps intracellular, chylous canals and by blood vessels. Intestine usually commencing in xiii, apparently sometimes in xii, xiv or xv ; typhlosole only rarely present. Hearts paired in x and xi. Holonephridial. Holandric

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[1] Professor Gates informs me, in correspondence, that he has designated *G. elegans* the type-species in MS.

[2] This variation occurs only intraspecifically, in *G. robustus*.

or exceptionally, but not certainly, metandric; testis-sacs apparently sometimes present; seminal vesicles a pair in each of ix and xii or in xii only, sometimes present in x and xi in addition to one or both of these. Prostates tubular, two pairs, the glandular parts lined by a single layer of cells. Ovaries and their funnels situated in xiii, exceptionally (abnormally ?) in xii. Spermathecae with or without diverticula; each restricted to the segment behind its pore.

Diagnostic Characters. The combination of the possession of a single mid-ventral oesophageal pouch and the presence of two pairs of prostatic pores on two consecutive segments with the male pores in or near the intermediate furrow.

Key to Species-groups within *Gordiodrilus* (s. mihi)

	Gizzard present	1
	Gizzard absent	2
1a	Gizzard in viii	***robustus*** species-groups, pp. 317
1b	Gizzard in vii only	***pampaninii*** species-group, pp. 319
2a	Vasa deferentia discharging through bursae copulatrices	***papillatus*** species-group, pp. 319
2b	No bursae copulatrices	3
3a	Prostatic pores paired in xvii and xviii or xviii and xix or in xviii only	***elegans*** species-group, pp. 306
3b	Prostatic pores paired in xx and xxi	***tenuis*** species-group, pp. 316

ELEGANS Species-group (see Jamieson, 1962*b*)

Representative species *Gordiodrilus elegans* Beddard, 1892; the type-species.

Definition. Small to medium-sized worms with 80 to 125 segments. Prostomium epi-, proepi-, or zygo-lobous. Setae uniform. Clitellum embracing part or the whole of xii or xiii or xiv to part or the whole of xvii or xviii or xix, usually commencing on xiii and ending on xviii or xix. Prostatic pores paired in each of xvii and xviii or xviii and xix, exceptionally[1] (abnormally ?) a pair in xviii only. Female pores anterior to the setal zone of xiv, exceptionally[2] posterior in this segment. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9, or exceptionally[3] one pair in (?) or just behind furrow 7/8, or none. No genital markings present. Dorsal pores at least sometimes present.

Gizzards absent. Oesophageal pouch not known to be paired; typhlosole absent (?). Holandric; testis-sacs apparently sometimes present. Spermathecal ducts only exceptionally very long and slender.

Diagnostic Characters. The combination of the absence of a gizzard, with a pair of prostate pores in xvii and xviii or xviii and xix.

Remarks. The *elegans* species-group appears to be a natural one although it is not homogeneous in some respects. It includes *G. bonacanus, chuni, dominicensis, habessinus, madagascariensis, paski, siwaensis, wemanus* and *zanzibaricus*, with prostatic pores in xvii and xviii; *G. ditheca* with prostates in xviii only; and *G. elegans, mobucanus, niloticus, travancorensis* and *worthingtoni* with prostatic pores in xviii and xix.

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[1] *G. ditheca.*
[2] *G. mobucanus.*
[3] *G. chuni.*

Until more extensive collections of this species-group are available it seems unlikely that the full synonymy of its species will be convincingly established. Nevertheless, recourse to type material has shown *G. unicus* and *G. peguanus* to belong in the synonymy of *G. paski* (see Jamieson, 1962*a*). Far wider synonymy probably exists. It has been suggested (Jamieson, 1962*b*) that *G. niloticus, G. worthingtoni* and *G. bonacanus* may belong in *G. travancorensis* and a possibility of their synonymy with *G. paski* is indicated by the suggestion of Cernosvitov (1942) that *unicus* (now in *paski*) *madagascariensis, travancorensis, bonacanus* and *dominicensis* may represent a single species and the placing by Gates (1954) of *bonacanus* in the synonymy of *peguanus* (now in *paski*).

Acceptance of all these synonymies would reduce the *elegans* species-group from fifteen to nine species and, by reducing the importance attached to certain characters for specific separation, would probably necessitate further suppression. Such extensive changes require more evidence than is yet available and in the present work only the synonymy of *peguanus* and *unicus* with *paski* is accepted.

Key to Species of the *ELEGANS* Species-group

1a	Prostatic pores two pairs	2
1b	Prostatic pores one pair (in xviii)	*G. ditheca*, p. 309
2a	Prostatic pores in xvii and xviii	3
2b	Prostatic pores in xviii and xix	10
3a	Spermathecal pores absent	*G. dominicensis*, p. 309
3b	Spermathecal pores one pair, in viii	*G. chuni*, p. 308
3c	Spermathecal pores two pairs	4
4a	Clitellum saddle-shaped	*G. bonacanus*, p. 308
4b	Clitellum ring-shaped	5
5a	A greatly raised tuberculum pubertatis present between the seminal grooves	*G. siwaensis*, p. 313
5b	No tuberculum between the seminal grooves	6
6a	Ventral surface of viii and of the anterior half of ix thickened and glandular	*G. zanzibaricus*, p. 316
6b	Ventral surface of viii neither thickened nor glandular	7
7a	Spermathecal ducts with diverticula	8
7b	Spermathecal ducts without diverticula	9
8a	Septa 5/6 to 9/10 thickened, 6/7 to 8/9 very strongly	*G. habessinus*, p. 310
8b	Septa never very strongly thickened	*G. paski*, p. 312
9a	Prostatic pores in setal lines *b*; the male genital field protuberant as an almost square area at fullest development from 16/17 to 18/19	*G. wemanus*, p. 315
9b	Prostatic pores just lateral to setal lines *b*; field not as above	*G. madagascariensis*, p. 311
10a	Spermathecal pores absent	*G. niloticus*, p. 312
10b	Spermathecal pores two pairs	11
11a	Spermathecal duct with diverticula	12
11b	Spermathecal duct without diverticula	13
12a	Prostatic pores in setal lines *b*	*G. worthingtoni*, p. 315
12b	Prostatic pores median to setal lines *a*	*G. elegans*, p. 310
13a	Female pores presetal in xiv	*G. travancorensis*, p. 314
13b	Female pores post-setal in xiv	*G. mobucanus*, p. 311

Gordiodrilus bonacanus Cernosvitov, 1942

Gordiodrilus bonacanus Cernosvitov, 1942. *Proc. zool. Soc. Lond.*, 1941 (B), **111**: 215–217, text-fig. 53–57.
Gordiodrilus bonacanus ; Jamieson, 1962*c*. *Ann. Mag. nat. Hist.*, (13), **5** : 47–49.
Gordiodrilus peguanus (part.) ; Gates, 1954. *Bull. Mus. comp. Zool. Harvard*, **111**, no. 6 : 246.

TYPE-LOCALITY : Bonaco Island, " 16° 30′ N. 85° 55′ W."

DEFINITION. Length 40 to 42 mm., diameter at the anterior end 1 mm., number of segments 85 to 91. Setae uniform ; in vii and xxxi to xxxv, *dd* = 0·5 *u*, *bc* = 1·2 *aa*. Clitellum saddle-shaped, embracing ½ xiii to ½ xix, the ventral surface in this region to a lesser degree glandular. Prostatic pores paired in xvii and xviii at the sites of the absent setae *b*, each on an almost circular, slightly raised papilla which extends laterally beyond setal line *b* and medially just includes seta *a* of its side ; the pores on each side connected by a fine, distinct seminal groove which is straight or perhaps slightly curved towards the midline and is intersected by three transverse medially unbroken furrows ; the first of these furrows posteriorly limiting the anterior prostate porophores, the second intersegmental and the third anteriorly limiting the posterior prostate porophores. Male pores probably at the intersection of the seminal grooves and intersegmental furrow 17/18, certainly not far removed from this situation ; the whole genital field distinctly protuberant. Female pores in setal lines *b*, or a little median of this, anterior in xiv. Spermathecal pores a pair in each of intersegmental furrows 7/8 and 8/9 in setal lines *b* ; each pore almost as wide as a setal couple.

Intestine commencing in xiii. Holandric with a pair of seminal vesicles in xii. Prostates with imperceptibly demarcated ducts. Spermathecae paired in viii and ix ; the efferent duct, which has a width in the middle region of 0·09 to 0·14 mm., distinctly demarcated from the subspherical ampulla, the width of which varies from 0·18 to 0·24 mm. The duct narrow, tubular, distally tapering and without diverticula ; or distinctly spindle-shaped with a minute knob-like diverticulum on each side of the equator.

Gordiodrilus chuni Michaelsen, 1913

Gordiodrilus chuni Michaelsen, 1913 : *Zoologica*. Stuttgart, H. **68** : 7–9, text-fig. 3, Taf. II, fig. 17.
Gordiodrilus chuni ; Jamieson, 1963. *Mitt. naturh. Mus. Hamburg*. **60**, Dec, 1962: 43–55.

TYPE-LOCALITY : Kandahar Island, some kilometres above the Victoria Falls, Rhodesia.

DEFINITION. Length 35 mm., diameter 1·1 mm., 87 to 95 segments. Setae : *dd* slightly less than 0·5 *u*, *bc* about equal to *aa* ; one or both members of each ventral couple present in xvii and xviii. Clitellum saddle-shaped with the ventral borders approximately in setal lines *b*, embracing xiii to xvi ventrally and xii to xvii dorsally. Prostatic pores paired in xvii and xviii, those of a side situated at the opposite ends of a conspicuously raised, longitudinally oval, glandular thickening of the skin. This extends from before the setal zone of xvii to behind that of xviii and is separated from its fellow of the other side by a region of similar width ; each thickening symmetrically cleft by a longitudinal seminal groove which connects the prostate pores and which lies just lateral to setal line *b* of the adjacent segments. Male pores each on a minute papilla at the intersection of the seminal and intersegmental furrows 17/18. Female pores somewhat lateral of setal line *b*, a little in front of the setal zone of xiv. Spermathecal pores a single pair just median to setal lines *c* and approximately midway between intersegmental furrow 7/8 and the setal zone of viii, or in the furrow and setal line *b*.

Holandric, with seminal vesicles in ix and xii. Prostate ducts unusually slender and abruptly demarcated. Ovaries (abnormally ?) in xii, oviducts normally situated. Bithecal; spermathecae consisting of an ampulla, 0·68 mm. long, made up of a proximal small spherical appendage which opens through a short duct into an inflated though slightly depressed region, 0·27 mm. wide, one side of which is faintly lobed, and a slender abruptly demarcated duct, 0·41 mm. long and 0·04 mm. wide, into which the latter opens ; the proximal part of the lobed region extending below the appendage ; or consisting in a thin-walled, tubular, sac-like ampulla which is slightly longer than the tubular bent duct from which it is clearly demarcated.

Gordiodrilus ditheca Beddard, 1892

Gordiodrilus ditheca Beddard, 1892. *Ann. Mag. nat. Hist.* (6), **10** : 90–91, Pl. VII, fig. 8.
Gordiodrilus ditheca; Beddard, 1895. A Monograph of the Order Oligochaeta : 509.
Gordiodrilus ditheca; Michaelsen, 1900. *Das Tierreich, Lief.* **10**, Vermes, Oligochaeta : 374.

TYPE-LOCALITY : Lagos, West Africa (?). Found in Kew Gardens, England.

DEFINITION. Clitellum embracing xiii to xvii. Spermatheca a single pair, without diverticula, opening in intersegmental furrow 7/8 (?) ; prostate glands a single pair opening in xviii. Otherwise as *G. elegans*.

Gordiodrilus dominicensis Beddard, 1892

Gordiodrilus dominicensis Beddard, 1892. *Ann. Mag. nat. Hist.* (6): **10**, 91–93, 94, 95, Pl. VI. fig. 2–3.
Gordiodrilus dominicensis ; Beddard, 1895. *A Monograph of the Order Oligochaeta*: 509.
Gordiodrilus dominicensis ; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta: 374.
Gordiodrilus dominicensis ; Beddard, 1901. *Proc. zool. Soc. Lond.* 1901, **1**: 364.
Gordiodrilus dominicensis ; Jamieson, 1962*c*. *Ann. Mag. nat. Hist.* (13), **5** : 50.
[non] *Gordiodrilus dominicensis* ; Michaelsen, 1914. *Mitt. naturh. Mus. Hamburg*, **31** : 109–110 (vide *G. niloticus*).

TYPE-LOCALITY : Dominica, West Indies (?). Found at Kew Gardens, England.

DEFINITION. Length 26 mm., diameter at the head end 1 mm., about 80 segments. Setae uniform ; the ventral pairs absent from xvii and xviii. Clitellum xiii to xviii ; spermathecal pores absent ; prostate pores paired in xvii and xviii, borne on two projecting (longitudinal ?) folds of epithelium. Intestine commencing in xiii. Holandric. No spermathecae.

Gordiodrilus elegans Beddard, 1892

Gordiodrilus elegans Beddard, 1892. *Ann. Mag. nat. Hist.* (6), **10** : 84–90, 94, 95, Pl. VI, fig. 1, Pl. VII, fig. 6A, 7.
Gordiodrilus elegans ; Beddard, 1895. *A Monograph of the Order Oligochaeta* : 508–509.
Gordiodrilus elegans ; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta : 374.
Gordiodrilus elegans ; Jamieson, 1962*c*. *Ann. Mag. nat. Hist.* (13), **5** : 53.

TYPE-LOCALITY : Lagos, West Africa (?). Found at Kew Gardens, England.

DEFINITION. Length ca. 40 mm. Setae uniform ; *a* and *b* of xviii (?) and xix (?) absent at maturity. Clitellum saddle-shaped, embracing xiii to xviii. Prostate pores paired in xviii and xix ; a male pore lying in intersegmental furrow 18/19 in line with, or perhaps just median to, and midway between those of each side. All three pores appreciably median to setal line *a* of the adjacent segments and situated near the lateral edges of a raised rectangular area, which extends anteriorly and posteriorly almost to the borders of xviii and xix and laterally approximately to setal lines *a* of the adjacent segments. The centre of this region is abruptly sunken so as to be surrounded by a ridge bearing the pores. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9.

Holandric with seminal vesicles in ix to xii. Prostate ducts abruptly demarcated. Spermathecae paired in viii and ix, rarely both pairs in viii ; each with a round or oval thin-walled ampulla and a narrow duct with a pair of rudimentary diverticula at their junction.

Gordiodrilus habessinus Michaelsen, 1913

Gordiodrilus habessinus Michaelsen, 1913. *Zoologica.* Stuttgart, H. **68** : 5–7, Taf. II, fig. 30–31, text-fig. 2.
Gordiodrilus habessinus ; Michaelsen, 1915. *Wiss. Ergebn. zw. dtsch. zent. Afr. Exped.* Band 1, Zool. 1, Teil. 1, Lief. 8, Oligochaeta : 218–219.
Gordiodrilus habessinus ; Jamieson, 1963. *Mitt. naturh. Mus. Hamburg.* **60**, Dec. 1962: 43–55.

TYPE-LOCALITY : Abyssinia.

OTHER LOCALITIES : Source of the River Shari, Fort Crampel, " ca. 7° N. 19° 20′ E.," Gribingi, French West Africa.

DEFINITION. Length 30 to 36 mm., maximum diameter 1 to 1·4 mm., ca. 80 to 110 segments. Setae : *dd* slightly smaller than $\frac{1}{2}$ *u*, *bc* ca. = 1·3 *aa* ; setae *b* and sometimes some of setae *a* absent from xvii and xviii ; setae *a* closer together in these segments than elsewhere. Clitellum ring-shaped, embracing segments $\frac{1}{3}$ xiii to $\frac{1}{3}$ xix. Male genital field at maturity strongly raised in the form of a right-angled cushion, wider than long, which extends over the entire lengths of xvii and xviii and laterally over setal lines *b*. The angles of the field each filled by an indistinct transverse papilla. Prostate pores paired in xvii and xviii at the sites of the absent setae *b* or just lateral to setal lines *b* ; those of each side interconnected by an almost straight seminal groove, which ends on the papilla of its side or, in the absence of the papillae (perhaps when less mature) connected by a laterally somewhat convex seminal groove rimmed by slight ridges surrounding the prostate pores. Male pores in the seminal grooves approximately where these are intersected by intersegmental furrow 17/18. Female pores anterior in xiv, just lateral to setal lines *b* which their median ends reach. Spermathecal pores paired in intersegmental furrosw 7/8 and 8/9 just lateral to or in setal lines *b*.

Holandric with seminal vesicles in ix and xii or (probably only when immature) in xii only; sperm masses in x and xi perhaps in vesicles also. Prostate glands unusually thin and with the duct about half the thickness of the glandular part. Ectal ends of the vasa deferentia unthickened. Spermathecae consisting of an ellipsoidal almost spherical ampulla and a sharply demarcated fairly stout cylindrical or spindle-shaped duct about as long as the ampulla; the duct bearing at different points three (or four ?) diverticula which are embedded in the glandular investment of the duct and are hardly visible externally.

Gordiodrilus madagascariensis Michaelsen, 1907

Gordiodrilus madagascariensis Michaelsen, 1907. Reise in Ostafrika in den Jahren 1903–1905, von A. Voeltzkow. Ergebn., II, *Syst. Arb.*, H.2: 46–47.

Gordiodrilus madagascariensis; Jamieson, 1963. *Mitt. naturh. Mus. Hamburg*. **60**, Dec. 1962: 43–55.

TYPE-LOCALITY: Madagascar: Fénérive (30 miles N. of Tamatave, 18° 8′ S· 49° 22′ E.) and Ambodifotra (16° 55′ S. 49° 52′ E.), Sainte Marie.

DEFINITION. Length 38 mm., diameter 1 mm., 115 segments. Setae uniform; *bc* slightly smaller than *aa* only in the first setigerous segment elsewhere larger; especially behind the clitellum where *bc* ca. = 7/5 *aa*; *dd* a little smaller than 0·5 *u*; ventral setae of xvii and xviii present. Clitellum ring-shaped, apparently less developed ventrally, embracing $\frac{1}{2}$ xiii to xix. Prostate pores paired in xvii (?) and xviii (?), the anterior immediately behind and the posterior just in front of the setal zone lateral to setal line *b*. Male pores immediately behind intersegmental furrow 17/18, roughly in line with the prostate pores. Female pores in front of setae *b* of xiv. Spermathecal pores a pair in or close behind each of intersegmental furrows 7/8 and 8/9, a little lateral to setal lines *b*.

Intestine commencing in xiv. Holandric with seminal vesicles in ix and xii. Prostate ducts not sharply demarcated. Ectal ends of the vasa deferentia not thickened. Spermathecae without diverticula, consisting of a large almost spherical ampulla and a long, thin, sharply demarcated duct of which the ectal end, running within the body wall, is sharply bent.

Gordiodrilus mobucanus Cognetti, 1907

Gordiodrilus mobucanus Cognetti, 1907*a*. *Boll. Mus. Zool. comp. Torino*, **22**, No. 551: 4.

Gordiodrilus mobucanus; Cognetti, 1907*b*. *Il Ruwenzori*: 383–384, Taf. III, fig. 43.

TYPE-LOCALITY: Mt. Ruwenzori, Mobuco Valley, East Africa.

DEFINITION. Length (immature) 65 mm., width 1·5 mm., 120 segments. Setae uniform; in the midbody *bc* ca. = 1·3 *aa*, *dd* = 0·5 *u*. Prostate pores paired in xviii and xix in the setal zones a little lateral of setal lines *b*; those of each side connected by a long, narrow, straight seminal groove which is bounded by a marked tumescence. Male pores in the seminal grooves at the posterior margin of xvii. Female pores at the posterior margin of xiv in setal strip *ab*, like the prostate pores not externally visible. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9 a little lateral of setal lines *b* on small tubercles.

Intestine commencing in xv. Holandric with seminal vesicles in ix and xii. Vasa deferentia of each side running close together and uniting near the male pore. Spermathecae almost tubular, a little dilated entally; without diverticula; paired in viii and ix.

Gordiodrilus niloticus Jamieson, 1962

Gordiodrilus niloticus Jamieson, 1962*b*. *Proc. zool. Soc. Lond.* **139**: 608.
(= *G. dominicensis*; Michaelsen, 1914. *Mitt. naturh. Mus. Hamburg*, **31** : 109–110; [non]. *G. dominicensis* Beddard, 1892).

Type-locality : 9° 30′ N. 31° E., on the White Nile, Tongo, Upper Nile Province, Sudan.

Definition. Length 28 to 50 mm., maximum diameter 1 to $1\frac{1}{4}$ mm., 87 to 125 segments. Setae fairly delicate and uniform (with the exception of those of xii which may be elongated ?); setae *b* absent from xviii and xix, where the distance between setae *a* is only two-thirds of that in xx; in xii *dd* ca. = 0·4 to 0·5 *u*, *bc* ca. = 1·3 to 1·5 *aa*. Clitellum saddle-shaped, anteriorly very protuberant; embracing xiii, $\frac{3}{4}$ xiii, $\frac{1}{2}$ xiii to $\frac{1}{2}$ xix, xix (minimally $6\frac{1}{2}$ segments). Prostate pores paired in xviii and xix at the sites of the absent setae *b*, each on a transversely oval papilla which extends laterally well beyond setal line *b* and medially just includes seta *a* of its side. The pores of each side connected by a fine, distinct seminal groove which is intersected by three transverse medially unbroken furrows; the first of these posteriorly limiting the anterior prostate porophores, the second intersegmental, and the third anteriorly limiting the posterior prostate porophores. Male pores at the intersection of seminal grooves and intersegmental furrow 18/19. Spermathecal pores absent.

Intestine commencing in xiii (?). Holandric with seminal vesicles in xii. Prostates with abruptly demarcated very narrow ducts. Vasa deferentia entering the body wall just behind septum 18/19.

Gordiodrilus paski Stephenson, 1928

Gordiodrilus paski Stephenson, 1928. *Ann. Mag. nat. Hist.* (10), **1** : 1–4, text-fig. 1.
Gordiodrilus unicus Stephenson, 1931. *Proc. zool. Soc. Lond.* 1931, **1** : 79–81, text-fig. 25.
Gordiodrilus peguanus Gates, 1942. *Bull. Mus. comp. Zool. Harvard*, **89**, No. 3 : 85–90.
Gordiodrilus peguanus (part.); Gates, 1954. *Bull. Mus. comp. Zool. Harvard*, **111**, No. 6 : 246 (excluding *G. bonacanus*.)
Gordiodrilus paski; (including *G. unicus* and *G. peguanus*) Jamieson, 1962*a*. *Ann. Mag. nat. Hist.* (13), **4**: 519–527.

Type-locality : Kigoma Harbour (4° 52′ S. 29° 38′ E.), Lake Tanganyika.

Other localities : Bhamo (24° 5′ N. 97° 5′ E.), Burma (Stephenson, 1931); Bangalore (12° 58′ N. 77° 35′ E.), India, and numerous localities in Burma (Gates, 1942); Rio Piedras, Porto Rico (Gates, 1954).

Definition. Length 35 to 47 mm., width 1 to 1·5 mm., about 98 segments. Setae uniform; in vii *dd* = 0·5 *u*, *bc* ca. = 1·1 *aa*; in xxv *dd* ca. = 0·4 *u*, *bc* = 1·3 *aa*;

ventral setae of the segments bearing the prostate pores all absent (merely obscured ?) or some of them present. Clitellum ring-shaped except sometimes in xvii and xviii, embracing ½ xiii, xiv (?) to xviii, 1/n xix, 1/n xx. Prostate pores paired in xvii and xviii in the setal zones in the immediate neighbourhood of the sites of the ventral setae, those of each side connected by a seminal groove which is straight or curves slightly outwards and which is often covered by the cuticle of the general body surface. The borders of the grooves sometimes very slightly raised especially at the extremities. The whole male genital field protruding as an approximately square area or consisting of a dumb-bell-shaped area bearing each groove and raised more noticeably at the pores than elsewhere. Male pores apparently situated at the intersection of the seminal grooves with intersegmental furrow 17/18. Female pores just lateral to setal lines *b* immediately behind intersegmental furrow 13/14. Spermathecal pores paired transverse slits in intersegmental furrows 7/8 and 8/9, the centres of which lie in or near setal lines *b*.

Intestine commencing in xii. Holandric with seminal vesicles in xii and sometimes also in ix and possibly testis-sacs in x and xi. Vasa deferentia on each side passing a little lateral of the prostate pores and entering the body wall midway between the corresponding prostates ; at least posteriorly single. Ducts of prostates more slender than the glandular parts but not sharply demarcated. Spermathecae paired in viii and ix, each with the form of an almost tubular sac which is bent a few times. The ental end of the sac may be swollen into a definite ampulla and is markedly swollen over a short region immediately ental to the fairly distinct remaining region which constitutes the duct. The walls of this swollen region (always ?) possess two to eight small chambers or diverticula. Length ampulla 0·2 mm., width ampulla and the swollen part of the duct 0·1 mm., width of the spermatheca ental to and ectal to the swollen portion 0·07 mm.

Gordiodrilus siwaensis Jamieson, 1962

Gordiodrilus sp. Michaelsen, 1937 (1938). *Proc. zool. Soc. Lond.* (B), **107**, pt. 4 : 509.
Gordiodrilus siwaensis Jamieson, 1962*b*. *Proc. zool. Soc. Lond.* **139** : 612.

TYPE-LOCALITY : Siwa Oasis, ca. 29° N. 26° E., Egypt.

DEFINITION. Length 37 mm., maximum diameter (at the clitellum) 1·3 mm., 90 segments. Setae apparently uniform ; in ix *dd* ca. = 0·5 *u*, *bc* ca. = 1·5 *aa* ; setae *b* of xvii and xviii absent, setae *a* closer together here than elsewhere. Clitellum ring-shaped, xiii (?), ½ xiii to ½ xix, anteriorly not protuberant, but recognizable by its brownish colour. Prostatic pores paired in xvii and xviii. A greatly raised tuberculum pubertatis lies ventrally in xvii and xviii, its rounded anterior and posterior ends pushing the setal ridges of these segments respectively anteriorly and posteriorly but just including setae *a* ; its lateral borders flanked by straight seminal grooves which lie in line with setae *a* of adjacent segments (not with those of xvii and xviii) and are terminated by the prostate pores. A low papilla fills each of the angles subtended by the border of the tuberculum and the bounding setal ridges and extends laterally to approximately midway between setal lines *b* and *c*. Male pores at the intersection of the seminal grooves and intersegmental furrow 17/18 (?). Female pores each on a small purplish, protuberant, transversely oval papilla, approximately as wide as a setal couple, the centre of which lies very slightly lateral to setal line *b* and a little nearer the setal zone of xiv than that of xiii. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9; each pore a transverse slit slightly wider than a setal couple, its centre just lateral to setal line *b*. The ventral surface of viii bearing a clitellum-like thickening which reaches laterally to setal lines *c*.

Intestine commencing in xiii. Holandric with seminal vesicles in xii (and ix ?). Prostate ducts not sharply demarcated from the tapering glandular parts. The double vas deferens of each side entering the body wall midway between the anterior and posterior prostate pores. Spermathecae paired in each of viii and ix, each consisting of an ovoid ampulla 0·24 mm. wide and 0·32 mm. long and a stout, strongly curved, slightly shorter duct distally 0·11 mm. wide; the duct swollen and spindle shaped owing to the presence of at least three evaginations of its walls, which are not externally visible because of a uniform (glandular ?) covering of the duct; each evagination apparently with the form of a narrow-based diverticulum and, like the ampulla, containing sperm.

Gordiodrilus travancorensis Michaelsen, 1910

Gordiodrilus travancorensis Michaelsen, 1910*a*. *Abh. naturw. Ver. Hamburg*, **19**, H.5 : 98–100.
Gordiodrilus travancorensis; Stephenson, 1923. *Fauna of British India*, Oligochaeta, London : 482–483.
Gordiodrilus travancorensis; Jamieson, 1963. *Mitt. naturh. Mus. Hamburg*. **60**, Dec. 1962: 43–55.

TYPE-LOCALITY: Nedumangad, 10 miles NE. of Trivandrum, 8° 29′ N. 76° 58′ E., Travancore, S. India.

DEFINITION. Length 32 mm., maximum diameter $\frac{2}{3}$ mm., 84 segments. Setae: in the forebody *dd* ca. = $\frac{1}{2}$ *u*; *bc* slightly smaller than *aa*; setae *b* of xviii and xix apparently absent. Clitellum saddle-shaped, or at least less well-developed between setal lines *a*, embracing $\frac{1}{4}$ xiii to xix (= 6$\frac{1}{2}$, *sic* Michaelsen) though much less developed in xix. Prostate pores paired in xviii and xix at the sites of the apparently absent setae *b*; each on a transversely oval, almost circular papilla which extends laterally beyond setal line *b* and medially just includes seta *a* of its side. The pores of each side connected by a fine distinct seminal groove which is intersected by three transverse medially unbroken furrows; the first of these posteriorly, limiting the anterior prostate porophores, the second intersegmental, and the third anteriorly, limiting the posterior prostate porophores. Male pores probably at the intersection of the seminal grooves and intersegmental furrow 18/19, certainly not far removed from this situation. Female pores anterior to setae *ab* of xiv. Spermathecal pores paired in each of intersegmental furrows 7/8 and 8/9 in setal lines *b*.

Intestine commencing between xii and xiii. Holandric, with seminal vesicles in xii. Prostate ducts little thinner than the glandular parts from which they are not abruptly demarcated. Vasa deferentia entering the body wall midway between the anterior and posterior prostate pores. Spermathecae in viii and ix, each consisting of a sac-like ampulla and a narrow duct of approximately the same length, or (only when immature ?) of an entally blind tube 0·27 mm. long and 0·09 mm. wide, the ental fourth of which forms a spherical ampulla marked off from the duct, which anteriorly tapers to about half the general width, by a faint constriction.

Gordiodrilus wemanus Michaelsen, 1937

Gordiodrilus wemanus Michaelsen, 1937. *Bull. Mus. comp. Zool. Harvard*, **79** : 446–449, fig. 8, 9.
Gordiodrilus wemanus; Jamieson, 1963. *Mitt. naturh. Mus. Hamburg.* **60**, Dec. 1962 : 43–55.

TYPE-LOCALITY : Wema, " ca. 02° 30′ S. 40° E.", Ngatana District, Tana River, Kenya.

DEFINITION. Length 35 to 45 mm., width 1·0 to 1·5 mm., segments 92 to about 120. Setae : *dd* = 0·4 to 0·5 *u*, *bc* greater than *aa* ; towards the clitellum the setae are apparently very slightly shifted ventralwards and moderately large, the ventral slightly larger than the lateral ; setae *b* of xvii and xviii apparently are always absent. Clitellum ring-shaped, embracing xii, xiii, xiv to xviii (?), $\frac{1}{4}$ xix, xix ; sometimes saddle-shaped behind the seminal grooves. Prostate pores paired in xvii and xviii in the setal zones and setal lines *b*, each at the centre of a more or less distinct circular porophore, those of each side connected by a straight or outwardly curving seminal groove, which is often covered by the cuticle of the body surface, and is bordered by lateral walls. The whole male genital field when fully developed projects as a squarish area extending between intersegmental furrows 16/17 and 18/19, and distinctly bordered on each side by a smooth, longitudinal, sometimes whitish elevation which lies slightly lateral of setal line *b*. Male pores in the seminal grooves at or very near the intersection with intersegmental furrow 17/18 and visible only in prepared sections. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9 in setal lines *b* or slightly lateral of this, not visible externally ; or transverse slit-like openings with swollen margins forming an ellipse.

Intestine commencing in xiii. Holandric, with seminal vesicles in ix and xii. Testis-sacs perhaps present. Vasa deferentia attenuated, those of each side uniting before opening through the male pore. Prostate ducts not abruptly demarcated from the glandular parts, but perceptibly narrowing and distinguishable by their muscular sheen. Spermathecae paired in viii and ix, each consisting of a small oval or inverted pyriform ampulla and a narrower, rather sharply demarcated duct which in the ental two-thirds is about half as wide as the ampulla and in the ectal third gradually narrows to the exterior. The lumen of this duct is a simple, narrow, straight canal only in the narrower ectal third ; in the ental two-thirds it meanders slightly and forms irregular convolutions. There are no diverticula. Length of ampulla 0·21 mm., width of ampulla 0·27 mm., length of duct equal to that of the ampulla or two or three times as great, greatest width of the duct 1·14 mm.

Gordiodrilus worthingtoni Jamieson, 1962

Gordiodrilus worthingtoni Jamieson, 1962*b*. *Proc. zool. Soc. Lond.* **139** : 615.

TYPE-LOCALITY : Lake Baringo, 00° 45′ N. 36° 10′ E., from a stream running into Lake Hannington, Tanganyika.

DEFINITION. Length ca. 55 mm., maximum diameter (at the clitellum) ca. 1·5 mm., ca. 100 segments. Setae uniform ; in segment 7 *dd* = 0·5 *u*, *bc* = 1·1 *aa* ;

in xviii and xix, setae *a* present, setae *b* apparently absent. Clitellum distinctly saddle-shaped, embracing xiii to ½ xix, indistinctly delimited posteriorly, its longitudinal borders just median to setal lines *a*. Male genital field differing from that described for *G. niloticus* only in the more tumescent borders of the seminal grooves; sites of the male pores not known. Female pores a pair in setal lines *b* just behind intersegmental furrow 13/14. Spermathecal pores a pair of small elliptical slits in each of intersegmental furrows 7/8 and 8/9 in setal lines *b* or perhaps very slightly median to this.

Intestine commencing in xiii. Holandric, with seminal vesicles in xii (not seen in ix or xi). Prostates with abruptly demarcated ducts. Spermathecae paired in viii and ix, each consisting in a large, irregular, sac-like, thin-walled ampulla and much narrower, although still fairly stout, abruptly demarcated duct of approximately the same length. The duct may be tortuous entally; it bears, embedded in the cellular investment of the spermatheca, two or more pouch-like, narrow-stalked diverticula at about the ental quarter. The length of these diverticula is approximately equal to the width of the more ectal widest region of the duct; the lumina of some of the diverticula are branched and all communicate with the lumen of the duct. Greatest width of the ampulla 0·3 mm., length of the duct (not extended) 0·43 mm., greatest width of the duct 0·07 mm.

Gordiodrilus zanzibaricus Beddard, 1894

Gordiodrilus zanzibaricus Beddard, 1894*a*. *Quart. J. micr. Sci.*, N.S. **36** : 252–254.
Gordiodrilus zanzibaricus; Beddard, 1895. *A Monograph of the Order Oligochaeta*, 509–510.
Gordiodrilus zanzibaricus; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta, pp. 374–375.
Gordiodrilus mathewsi Beddard, 1895: *ibid.*: 453 [*Lapsus calami* for *G. zanzibaricus*, see Beddard, 1901, *Proc. zool. Soc. Lond.* 1901, **1** : 364, footnote].
Gordiodrilus zanzibaricus; Jamieson, 1962*c*. *Ann. Mag. nat. Hist.* (13), **5**: 51–52.

TYPE-LOCALITY: Zanzibar.

DEFINITION. Length ca. 25 mm. Setae all ventral; *bc* = *aa*; setae *a* (?) of xvii and xviii absent. Clitellum annular, ½ xiii to ¼ xix ?, xix. Prostate pores paired in xvii and xviii, those of each side connected by a seminal groove with raised somewhat folded margins. Male pores in intersegmental furrow 17/18 (?). Female pores immediately lateral to and at least sometimes (probably always) in front of setae *b* of xiv. Spermathecal pores paired in intersegmental furrows 7/8 and 8/9 a little lateral to setal lines *b*. The ventral surface of viii and that of the anterior half of ix modified, the epidermal cells being tall and glandular.

Intestine commencing in xiii. Holandric, with seminal vesicles in xii. Prostate ducts short and about half as wide as the glandular parts. Spermathecae a pair in each of viii and ix each with a peg-shaped ampulla from which a relatively much thinner duct penetrates the body wall.

TENUIS Species-group

Monotypic, containing *G. tenuis* Beddard, 1892.

DEFINITION. As for the species.

DIAGNOSTIC CHARACTERS. The far posterior position of the male and prostatic pores (xx and xxi) and the great length of the clitellum (xiv to xxvii).

REMARKS. (See also p. 303.) These characters taken with the possible metandry and the setal disparity suggest that *tenuis* should be given generic rank. The setal disparity is shared with the *papillatus* species-group.

Gordiodrilus tenuis Beddard, 1892

Gordiodrilus tenuis Beddard, 1892. *Ann. Mag. nat. Hist.* (6), **10** : 75–82, 94, 95, Pl. VII, fig. 6C.
Gordiodrilus tenuis; Beddard, 1895. *A Monograph of the Order Oligochaeta* : 507–508.
Gordiodrilus tenuis; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, Oligochaeta : 373.
Gordiodrilus tenuis; Jamieson, 1962*c*. *Ann. Mag. nat. Hist.* (13), **5** : 53–54.

TYPE-LOCALITY : Asaba, 75 miles E. of Benin, 6° 10′ N. 5° 38′ E., West Africa (?). Found at Kew Gardens.

DEFINITION. Length 90 mm., width 1 mm. The lateral setae about one fourth of the size of the ventral setae ; setae *a* rather larger than setae *b* ; the ventral setae present in the genital segments. Clitellum, visible only in prepared sections, saddle-shaped, embracing xiv to xxvii. Prostate pores paired in xx and xxi behind the setal zones. Male pores in front of the setal zone of xxi just lateral of setal lines *b*.

Intestine without typhlosole. Metandric (?). Seminal vesicles in x to xiii approximately. Vas deferens single on each side of the body, opening to the exterior not far behind the anterior septum of xxi after running closely adherent to the body wall. Prostates with rather short muscular ducts. Spermathecae paired in viii and ix, large and oval, each narrowing abruptly to form a very slender duct of considerable length ; without diverticula.

ROBUSTUS Species-group

Monotypic, containing *G. robustus* Beddard, 1892.

DEFINITION. As for the species.

DIAGNOSTIC CHARACTERS. The possession of a gizzard in viii, of an unpaired genital marking in xix, and of spermathecae in vii.

REMARKS. The reasons for restricting this group to *G. robustus* alone and for retaining it in *Gordiodrilus* are given on pp. 304 and 321.

Gordiodrilus robustus Beddard, 1892

Gordiodrilus robustus Beddard, 1892. *Ann. Mag. nat. Hist.* (6), **10** : 82–84, 94, 95, Pl. 7, fig. 4, 5, 6B.
Gordiodrilus robustus ; Beddard, 1895. *A Monograph of the Order Oligochaeta* : 508.
Gordiodrilus robustus ; Michaelsen, 1900. *Das Tierreich*, Lief. **10**, Vermes, *Oligochaeta* : 374.
Gordiodrilus robustus ; Beddard, 1901. *Proc. zool. Soc. Lond.* 1901, **1** : 363–365.
Gordiodrilus robustus ; Michaelsen, 1910*b*. *Wiss. Ergebn. dtsch. zent. Afr. Exped.*, **3**, Zool. 1, Lief. **1** : 114.
Gordiodrilus robustus congicus Michaelsen, 1936. *Rev. Zool. Bot. Afr.*, Tervueren, **29** : 47–52.
Gordiodrilus robustus ; (suppressing *congicus*) Jamieson, 1963. *Mitt. naturh. Mus. Hamburg.* **60**, Dec, 1962 : 43–55.

Type-locality : Lagos, West Africa (?). Found at Kew Gardens, England.

Other localities : Lagos (Beddard, 1901) ; from between Warri, 32° N. 5° 44′ E., and Sapela (28 miles N. of Warri), and also at Benin, 6° 10′ N. 5° 38′ E., Nigeria, and from Debundscha, 4° 7′ N. 8° 58′ E., at the foot of the Cameroon Mountains (Michaelsen, 1910) ; Leopoldville, " ca. 4° 47′ S. 15° 16′ E.", Belgian Congo (Michaelsen, 1936).

Definition. Length 32 to 72 mm., greatest width 2·0 mm., 90–125 segments. The posterior extremity, for about nine segments (always ?) swollen so that the hind end appears club-like. Unmodified setae, in front of v, 0·18 mm. long and 0·01 mm. thick, distinctly S-shaped with prominent node somewhat distal of the middle ; those of v to viii, or some of these segments, enlarged, as are those of the club-shaped region of the hind end, reaching 0·55 mm. in length and 0·03 to 0·04 mm. in width, the largest being the ventral setae of the last eight or nine segments ; the lateral setae of these segments very slightly smaller. The enlarged setae slightly S-shaped, with indistinct node somewhat ectal from the middle, their ectal ends slightly depressed in one plane and the terminal eighth ornamented with irregular scalloped tracts. The ventral setae of xii and xiii also enlarged, three or four times as large as the lateral setae of their segments, ca. 0·5 mm. long and 0·04 mm. thick ; similar in form and ornamentation to the other enlarged setae but perhaps less curved ; markedly shifted ventralwards, the skin in their vicinity apparently glandular ; the ventral setae of xi also surrounded by a glandular region slightly if at all displaced. In vii dd = 0·4 to 0·5 u, bc = 0·8 to 1·0 aa, the distance between the setal pairs several times that between the members of a pair, e.g. $aa : ab$ usually is about equal to 5 ; in the third segment from the posterior end, dd = 0·5 u, bc = 0·7 to 1·0 aa, the distance between the setal pairs being maximally twice that between the members of a pair, e.g. $aa : ab$ is about equal to 2. Clitellum saddle-shaped and protuberant, embracing $\frac{1}{2}$ xiii, $\frac{1}{4}$ xiii, xiv to xvi, $\frac{1}{2}$ xvii, 1/n xvii, xvii (= $3\frac{3}{4}$ to $4\frac{1}{2}$), with its straight, distinct, ventral margins just lateral to or including setal lines b. Prostate pores paired in xvii and xviii just lateral to and sometimes slightly behind setae b on diffuse low porophores which include the ventral setae, those of each side connected by a seminal groove which curves slightly medianwards and which runs approximately in setal lines b. Male pores in the seminal grooves just behind intersegmental furrow 17/18. A median tuberculum pubertatis longitudinally fills the anterior half of xix, reaches laterally slightly beyond setal lines a and anteriorly projects slightly over its anterior border. Female pores a pair of transverse slits of little extent lying midway between the setal zone of xiv and its anterior border, immediately lateral to setal lines b. Spermathecal pores minute, paired in intersegmental furrows 6/7 and 7/8 a little lateral of setal lines a.

Oesophagus with a well-developed gizzard in viii and (always ?) a rudimentary gizzard in vii ; a wholly or partly paired oesophageal sac dependent midventrally from the oesophagus in ix ; intestine commencing apparently in xii, possessing a typhlosole from approximately xvii posteriorly. Holandric, with seminal vesicles in xi and xii. Prostates frequently confined to the segments in which they open, the duct imperceptibly demarcated. Spermathecae paired in vii and viii ; each consisting of a crumpled sub-spherical ampulla and an extraordinarily long and thin, anteriorly running duct which is sometimes coiled. There are no spermathecal diverticula. Width ampulla 0·35 to 1·5 mm., length duct 1·35 to 1·75 mm., width duct 0·03 to 0·05 mm.

PAMPANINII Species-group

Monotypic, containing *Gordiodrilus pampaninii* Baldasseroni, 1913.

DEFINITION. As for the species.

DIAGNOSTIC CHARACTERS. Restriction of the gizzard to vii.

REMARKS. The phylogenetic basis for exclusion of the single species of this species-group from Gates' *robustus* division is discussed on p. 322. The fact that the group is monotypic makes it impossible, as with the *robustus* species-group, to distinguish between group and specific characters.

Gordiodrilus pampaninii Baldasseroni, 1913

Gordiodrilus pampaninii Baldasseroni, 1913. *Monit. Zool. It. Firence*, **24** : 127–129.

TYPE-LOCALITY : Tarhuna (40 miles SE. of Tripoli, 32° 52′ N. 13° 12′ E.), Tripolitania.

DEFINITION. Length 37 mm., width 1·7 mm., 84 to 87 segments. Setae uniform ; *dd* = 0·5 *u*, *bc* less than *aa*. Clitellum saddle-shaped, embracing xiii to xix, very prominent dorsally ; the longitudinal margins in setal lines *b*. Prostate pores not visible externally, paired in xviii and xix ; those of each side connected by a distinct seminal groove which runs in setal line *b* in xvii to xix on a marked tumescence. Male pores not externally visible, one lying in each seminal groove at the posterior margin of xviii. Female pores also not seen, situated in xiv in line with the ventral setae. Spermathecal pores clearly visible in intersegmental furrows 7/8 and 8/9. Three midventral pairs of very swollen papillae with whitish centres present in xx, xxi and xxii, extending over the posterior borders of these segments ; the posterior pair absent in one of the two syntypes.

Oesophagus with a well-developed gizzard in vii. Holandric, with seminal vesicles in x, xi and xii. Prostates greatly elongated with the ducts much narrower than the glandular part. Spermathecae two pairs, in viii and ix. Those of viii small and pear-shaped with long, very slender, muscular ducts ; those of ix larger, spherical with crumpled surfaces, opening by similar ducts ; without diverticula.

PAPILLATUS Species-group

Monotypic, containing *Gordiodrilus papillatus* Beddard, 1901.

DEFINITION. As for the species.

DIAGNOSTIC CHARACTER. The presence of bursae copulatrices.

REMARKS. This monotypic group is similar to the *robustus* and *pampaninii* species-groups in having genital markings behind the prostatic segments and in the form of the spermathecae. It is unique within the restricted *Gordiodrilus* in having bursae copulatrices and this, combined with the setal disparity in each segment, suggests relationship with *Nannodrilus*. It is retained in *Gordiodrilus* because of the arrangement of the male and prostatic pores. The affinities of *G. papillatus* are discussed on p. 321.

Gordiodrilus papillatus Beddard, 1901

Gordiodrilus papillatus Beddard, 1901. *Proc. zool. Soc. Lond.* 1901, **1** : 358–363, text-fig. 88.

TYPE-LOCALITY : The neighbourhood of Lagos, 6° 29′ N. 3° 30′ E., West Africa.

DEFINITION. Length 63 mm., diameter 1·5 to 2·8 mm. (the latter measurement at the clitellum). The ventral setae much more marked than the lateral, especially in the five segments in front of the male genital pores, where they appear as strong hooks to the naked eye, and to a lesser extent in the last body segments ; one member of each ventral couple absent in the genital region. Clitellum annular (?), embracing xviii (?) to xxii (?). Prostate pores paired in xix (?) and xx (?) which are swollen relative to the other segments ; those of each side connected by, and terminating, a straight terminally somewhat widened seminal groove, ca. 1·8 mm. long. Each groove is bounded by tumid lip-like areas, ca. 3·3 mm. long, which are rounded anteriorly and posteriorly and narrow midway between the pores. Four pairs of small whitish papillae, each with a dark centre, lie immediately median to the tumid areas, the pairs lying in single file. A midventral papilla is present in each of three consecutive segments which are separated from the posterior prostate segment by four segments. The male pores open midway between the prostate pores.

Holandric, with seminal vesicles in ix, x and xi. Prostate ducts short and narrow. Vasa deferentia of each side uniting a segment or two before they enter a large spherical muscular terminal bulbus. Spermathecae paired in viii and ix, each with an oval sac-like ampulla and an unusually long, very slender duct.

PHYLOGENETIC CONSIDERATIONS

Stephenson (1930) accepted Michaelsen's suggestion that *Notiodrilus* (Acanthodrilinae) represents the ancestor of the Megascolecidae. *Notiodrilus* (since suppressed) is quadriprostatic with a pair of prostate pores in each of the segments xvii and xix with the male pores intermediate in xviii.

Gates (1942, p. 66) in discussing characters of the alimentary canal in the Ocnerodrilinae, concluded that there are grounds for regarding the Ocnerodrilinae as more primitive than the Acanthodrilinae. Moreover, by presenting evidence in support of the derivation of his *zanzibaricus* and *travancorensis* groups and *Nannodrilus* and *robustus* divisions of *Gordiodrilus* from a sexprostatic form, he further discredited the *Notiodrilus* theory.

In view of the importance of any evidence which contradicts the classical *Notiodrilus* theory a short discussion of *Gordiodrilus* and *Nannodrilus* as defined in this revision seems desirable. Conclusions from a survey of the six species here included in *Nannodrilus* support Gates' contention that it is primarily sexprostatic. The genus is remarkably homogeneous : interspecific variation in the male and prostatic terminalia is no greater than that which occurs intraspecifically, as in *N. schubotzi* and *N. staudei*, and homogeneity in the somatic systems is as striking as that in the genital systems. Thus *johneni*, *phreoryctes*, *schubotzi* and *togoensis* are all described as exhibiting a disparity in the size of the setae in each segment, the ventral being much larger than the lateral. Only in *N. africanus* is the existence of this setal disparity questionable ; it is not mentioned for *staudei* but the latter species is said to differ from *schubotzi* only in certain non-setal characters. The size of setae is not mentioned in any description of *N. africanus* and I find the type-specimens to have uniform setae, but all are immature. In all species except *africanus* the spermathecae are a pair in each of segments viii and ix or in viii only, and in all except *togoensis* and *johneni* a gizzard is present in vii and viii.

It is here tentatively suggested that the ancestral *Nannodrilus* had a pair of prostates opening to the exterior approximately equatorially in each of segments xvii, xviii and xix, the middle pair of which communicated with the exterior through or in common with the muscular bursae of the vasa deferentia ; possessed a strong gizzard in each of segments vii and viii ; spermathecae in each of segments viii and ix ; and exhibited setal disparity throughout the body. There was perhaps also a pair of spermathecae in vii, as is questionably the case in *N. africanus*.

The ancestral *Nannodrilus* here postulated does not seem too speculative. From it all known species of the genus can be derived by morphological variation which is evident in the extant species, and these species it closely resembles.

It is generally accepted (Stephenson, 1930, p. 820, 832) that fusion of male pores with prostatic pores is secondary to their separation. The ancestral *Nannodrilus* may, therefore, have been preceded by a form in which the male and prostatic pores in xviii were separate. Conditions prevailing in the Ocnerodrilinae suggest that these pores were situated equatorially in their segment rather than intersegmentally. This pre-*Nannodrilus* form may have possessed male ducts with unthickened ends. (Variation from thickened to unthickened ducts occurs among species of *Pygmaeodrilus*, *Nematogenia*, *Ilyogenia*, *Quechuona* (?) and *Malabaria* (?).) Such a form, with unthickened ducts, could give the arrangement of terminalia seen in Gates' *zanzibaricus* group by " elimination of the prostates of xix and dislocation anteriorly of the male pores to points midway between the remaining prostatic apertures " and in his *travancorensis* group by " suppression of the prostates in xvii and the dislocation posteriorly of the male pores ", the changes advanced by Gates (1942) when he derived these groups from his (undefined) sexprostatic ancestor. Concomitant with these changes would be loss of the spermathecae of vii and of the gizzards. (For reasons for combining these groups in the *elegans* species-group see p. 304.)

G. papillatus, which shares with *Nannodrilus* the possession of bursae copulatrices and setal disparity may be closer to *Nannodrilus* than it is to *Gordiodrilus*, the absence of gizzards and the presence of the gordiodriline arrangement of terminalia being possibly convergent similarities. Prostates in xix and xx cannot be explained, however, without additional hypotheses.

G. robustus may be derived from a pre-*Nannodrilus* form with unthickened male terminalia by changes similar to those producing *zanzibaricus* group species but with loss, this time, of the spermathecae of ix and retention of the gizzard in vii and viii; and *G. pampaninii* by changes like those producing *travancorensis* group species but with retention of the gizzard in vii. *G. tenuis* could be derived from the same form but, like *papillatus*, it has the male terminalia outside xvii to xix (and setal disparity) and its origins are obscure.

The existence in the Ocnerodrilinae of prostates or prostate-like organs in xix and xx, in *G. papillatus* ; xx and xxi in *G. tenuis* ; xvii and xx in *Malabaria paludicola* Stephenson, 1924 ; xvii, xix and xx in *Thatonia parva* Gates, 1945 ; xvii, xix, xx and xxi in *Eukerria peguana* Gates, 1942, and in *Deccania alba* Gates, 1949 ; and xvi, xvii and xviii in *Diaphorodrilus doriae* suggests that we may have to consider the possibility of origin of the Ocnerodrilinae, and probably of the Megascolecidae as a whole, from forms with a more extensive series of prostates even than has been postulated by Gates and myself in the sexprostatic precursors of *Gordiodrilus* and *Nannodrilus*. Certainly the validity of *Notiodrilus* or a similar quadriprostatic form as an ancestor of these species, and therefore of the family, is highly suspect.

REFERENCES

Baldasseroni, V. 1913. Lombrichi della Tripolitania. *Monit. zool. Ital. Firence,* **24** : 127–130.

Beddard, F. E. 1892. On a new genus of Oligochaeta comprising five new species belonging to the family Ocnerodrilidae. *Ann. Mag. nat. Hist.* (6), **10** : 74–97.

—— 1894*a*. A contribution to our knowledge of the Oligochaeta of Tropical Eastern Africa. *Quart. J. micr. Sci.* (*New Series*), **36** : 201–270.

—— 1894*b*. On two genera, comprising three new species of earthworms from Western Tropical Africa. *Proc. zool. Soc. London,* 1894 : 379–390.

—— 1895. *A Monograph of the Order Oligochaeta,* Oxford, Clarendon Press.

—— 1901. On some earthworms from British East Africa, etc. *Proc. zool. Soc. London,* 1901, **1** : 336–365.

Cernosvitov, L. 1942. Oligochaeta from various parts of the world. *Proc. zool. Soc. London,* 1941 (B), **111**, 1942 : 197–236.

Cognetti de Martiis, L. 1907*a*. Spedizione al Ruwenzori di S.A.R. Luigi Amedeo di Savoia Duca degli Abruzzi. Diagnosi preliminari. *Boll. Mus. Zool. comp. Torino,* **22**, No. 551, 1907 : 127–130.

—— 1907*b*. *Il Ruwenzori,* 383–384.

—— 1910. Lombrichi Africani. *Ann. Mus. civ. nat. Genova* (3), **4**.

Gates, G. E. 1942. Notes on various peregrine earthworms. *Bull. Mus. comp. Zool. Harvard,* **89**, No. 3 : 63–144.

—— 1945. On some Indian earthworms *Proc. Ind. Acad. Sci.* **21** B : 208–258.

—— 1949. On some Indian Ocneridrilids. *Proc. Ind. Acad. Sci.*, **30** B (5), 1949 : 279–283.

—— 1954. Exotic earthworms of the United States. *Bull. Mus. comp. Zool. Harvard,* **111**, No. 6 : 219–258.

——1957. Contribution to a revision of the earthworm family Ocnerodrilidae. The genus *Nematogenia. Bull. Mus. comp. Zool. Harvard,* **117**, No. 4 : 427–445.

Jamieson, B. G. M. 1962*a*. A redescription of *Gordiodrilus paski* Stephenson (Oligochaeta). *Ann. Mag. nat. Hist.* Ser. 13, **4** : 519–527.

——1962*b*. Some new species of Ocnerodrilinae (Oligochaeta). *Proc. zool. Soc. London,* **139** : 607–626.

—— 1962*c*. Material of *Gordiodrilus* (Oligochaeta) in the British Museum (Natural History). *Ann. Mag. nat. Hist.*, (13), **5** : 47–55.

——1963. Material of *Gordiodrilus* (Oligochaeta) in the Zoological Museum, Hamburg. *Mitt. naturh. Mus. Hamburg,* **60**, Dec. 1962 : 43–55.

MICHAELSEN, W. 1897. Neue und wenig bekannte afrikanische Terricolen. *Mitt. naturh. Mus. Hamburg*, **14**, 2 : 1–71.

—— 1900. Das Tierreich, Lief. **10**, *Vermes Oligochaeta*, Berlin.

—— 1903. Westafrikanische Oligochaeten, gesammelt von Herrn. Prof. Yngve Sjöstedt. *Arkiv. Zool.* **1** : 157–169.

—— 1907. Oligochaeten von Madagaskar, den Comoren und anderen Inseln des westlichen Indischen Ozeans. *Reise in Ostafrika* v. A. Voeltzkoew, Bd. 2, Stuttgart, 1907 : 39–50.

—— 1910*a*. Die Oligochätenfauna der vorderindisch-ceylonischen Region. *Abh. naturw. Ver. Hamburg*, **19**, H.5 : 1–108.

——1910*b*. Die Oligochäten des inneren Ostafrikas und ihre geographischen Beziehungen. *Wiss. Ergebn. dtsch. zent. Afr. Exped.* **3**, Zool. 1, Lief. 1 : 1–90.

—— 1913. Oligochäten vom tropischen und südlich-subtropischen Afrika. II. *Zoologica*, Stuttgart, Heft. 68 : 1–63.

—— 1914. Oligochaeten vom tropischen Afrika. *Mitt. naturh. Mus. Hamburg*, **31** : 81–127.

—— 1915. Oligochäten in, *Wiss. Ergebn. zw. dtsch. zent. Afr. Exped.*, Band 1, Zool. 1, Teil 1, Lief. 8.

——1933. Opisthopore Oligochäten aus dem mittleren und dem südlichen Afrika hauptsächlich gesammelt von Dr. F. Haas während der Schomburgh-Expedition 1931–32. *Abh. senk. nat. Ges.* **40**, H.4 : 411–433

—— 1936. Oligochaten von Belgish-Kongo, III. *Rev. Zool. Bot. Afr.*, Tervueren, **29** : 213–225.

—— 1937. Scientific results of an expedition to rain forest regions in Eastern Africa. VIII. Oligochaeta. *Bull. Mus. comp. Zool. Harvard*, **79** : 433–477.

—— 1938. On a collection of African Oligochaeta in the British Museum. *Proc. zool. Soc. London* (B), **107**, pt. 4, 1937 : 501–528.

STEPHENSON, J. 1924. On some Indian Oligochaeta, with a description of two new genera of Ocnerodrilinae. *Rec. Ind. Mus.* **25**, pt. IV : 317–365.

—— 1928. Oligochaeta from Lake Tanganyika (Dr. C. Christy's Expedition, 1926). *Ann. Mag. nat. Hist.* (10), **1**, No. 1 : 1–17.

—— 1930. *The Oligochaeta.* Oxford.

—— 1931. Oligochaeta from Burma, Kenya, and other parts of the world. *Proc. zool. Soc. London*, 1931, **1** : 33–92.

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ASSOCIATED WITH COPRID BEETLES IN THE COLLECTIONS OF THE BRITISH MUSEUM (NATURAL HISTORY)

BRITISH MUSEUM NATURAL HISTORY

G. OWEN EVANS and K. H. HYATT

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INTRODUCTION

FEMALES of the coprophilous species of *Macrocheles* are faculatively parthenogenetic (arrhenotokous) and display a phoretic association with insects, particularly coprid beetles. The genus is world wide in distribution and, at present, contains a greater number of species than any other in the Mesostigmata. The majority of the known species have been described by Berlese (1903, 1910, 1918) but, unfortunately, the inadequacy of the descriptions, which are rarely accompanied by illustrations, has made the identification of many of the species so difficult that Berlese's basic work has acted more as a deterrent than a stimulant to subsequent taxonomic studies.

The forty-six species dealt with in the present work have been collected from coprid beetles in the collections of the Department of Entomology, British Museum (Natural History). The mites were relaxed in 60% lactic acid before study. Type material is deposited in the British Museum (Natural History).

CLASSIFICATION

The genus *Macrocheles* contains the majority of the described species of the family Macrochelidae. Attempts at a division of the genus into more workable units have not altogether been successful owing to the high degree of morphological homogeneity displayed by its members. Evans & Browning (1956) and Evans (1956) were unable to find reliable criteria for distinguishing *Coprholaspis* Berl., *Nothrholaspis* Berl., *Holocelaeno* Berl., *Dissoloncha* Falconer, *Monoplites* Hull and *Neholaspis* Turk, from *Macrocheles*, although, recently, Filipponi & Pegazzano (1960) have proposed the genus *Glyptholaspis* to accommodate four species originally ascribed to *Macrocheles*, and Krantz (1962) has given generic status to *Holocelaeno*. The genus *Glyptholaspis* is characterized by the degree of sclerotization of the idiosoma and the sculpturing of the dorsal and sternal shields. Species of *Holocelaeno* differ from those of *Macrocheles* in the form of the cheliceral brush. Before considering the classification of the insecticolous members of the genus *Macrocheles* it seems appropriate to review the morphological criteria at present used in the classification of females of the group.

The chelicerae of the species associated with Coleoptera show a remarkable constancy in digital dentition, probably the result of adaptation for grasping stiff bristles in the region of the mouthparts of the insect. The digits are relatively short and stout, and the most characteristic feature of the dentition is the presence of a large backwardly directed tooth on the fixed digit and a stout bicuspid tooth on the movable digit (Text-fig. 9). The bicuspid tooth opposes a deep cleft behind the large tooth on the fixed digit. The insectan bristle lies in the cleft on the fixed digit and is held firmly by the bicuspid tooth. In free-living members of the genus the digits are usually longer and thinner and their dentition is more variable. The characteristic gripping mechanism of the insecticolous forms is poorly developed or lacking. A *pilus dentilis*, a dorsal seta, and two lyriform fissures are always present. The arthrodial membrane at the base of the movable digit is produced into one or two brush-like processes (Text-fig. 9). One " brush " is invariably strongly developed and in the *Holocelaeno*-group its filaments are extremely long, surpassing the tip of the digit (Text-fig. 136). The form of the gnathosomal base, hypostome and pedipalps, shows little interspecific variation. The corniculi are horn-like and subparallel and there are five or six, rarely seven, transverse rows of deutosternal denticles. Each pedipalp has five free segments, excluding a three-tined seta-like apotele, and the ontogenetic development of its chaetotaxy is normal ; the adult complement being 2–5–6–14–15. The tectum is basically tripartite (Text-fig. 69) except in *Macrocheles superbus* Hull which has a unipartite tectum.

The development of the sclerotization and chaetotaxy of the dorsum of the idiosoma during ontogeny is relatively constant. There appear to be no distinct sclerotized areas in the larva, but the podosomatal region bears the normal nine pairs of setae, and the opisthosomatal region five pairs. A large podonotal shield is present in the protonymph and carries 11 setae. The opisthonotal shield is also relatively large and bears eight or nine pairs of setae, comprising two or three pairs in the J-series, three pairs in the Z-series, and three pairs in the S-series. The deutonymphal dorsal shield is incised laterally at the juncture of the podonotal and opisthonotal elements. The region anterior to the incisions is provided with 18 pairs of setae and the posterior region, 10 or 11 pairs, depending on the presence of two or three setae of the J-series. Complete fusion of the podonotal and opisthonotal shields occurs in the adult which retains the deutonymphal chaetotaxy. We have adopted the system used by Hirschmann (1957) for the nomenclature of the dorsal setae (Text-fig. 1). There is a wide range of setal forms. The majority of the species have simple or finely pilose setae, but coarsely serrated and plumose dorsal setae may occur. The verticals (i1) and Z5 often differ in form from each other and from other dorsal setae. The dorsal shield is usually provided with 22 pairs of pore-like structures, and its surface may be smooth, punctate, areolate, or reticulate.

The tritosternum is biramous, the base being longer than wide and the laciniae pilose. There is considerable variation in the size and ornamentation of the sternal shield which bears the normal three pairs of setae. In the forms associated with Coleoptera and other insects the sternal shield extends to the level of the middle of coxae III. Its posterior margin and, more rarely, its anterior margin, may be deeply incised to give the sternal shield a strip-like appearance as in *M. spectandus*. The shield is more heavily sclerotized in free-living members of the complex. In the *Glyptholaspis*-group it is fused postero-laterally with the endopodal elements and extends to the level of the posterior margin of coxae III. The surface of the sternal shield may be smooth, punctate, areolate, or reticulate. Many insecticolous species have well-defined structural lines, the most important of which are the *linea media transversa* connecting the bases of sternal setae II and the *linea arcuata*. Berlese (1918) used the ornamentation of the sternal shield as the criterion for subdividing his subgenus *Coprholaspis* into phalanges, but this system has not been generally adopted owing to the difficulty of characterizing the ornamentation.

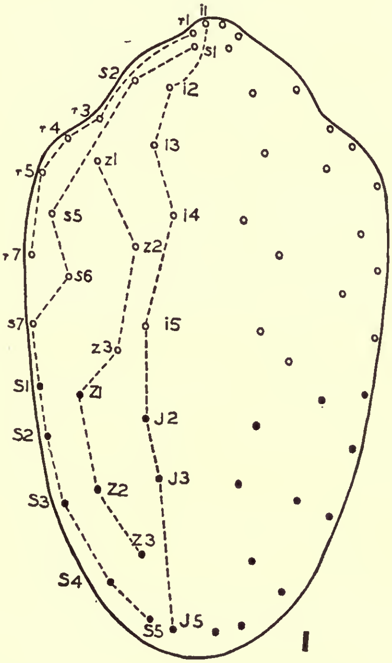


FIG. 1. Nomenclature for the chaetotaxy of the dorsal shield in the adults of *Macrocheles* Latr.

The genital shield has a pair of setae and is always provided with accessory sclerites. Its posterior margin is usually truncate. All species have a ventri-anal shield bearing from one to three pairs of pre-anal setae in addition to the three setae normally associated with the anal opening. There are no euanal setae. Neotrichy of the unsclerotized integument of the venter of the opisthosoma is not uncommon.

The peritrematal shield is free posteriorly and the peritreme forms a U-shaped loop on leaving the large stigma.

The legs are six segmented, excluding the ambulacrum. Lyriform fissures occur in the femora and tarsi of all legs, and those on the femora and the proximal part of the tarsi form false divisions of the segments. Legs I lack ambulacra but those on legs II–IV each comprises a lobate pulvillus and two claws. The lateral processes of the ambulacra show considerable variation in length, and may be simple or divided distally. They tend to be longer in the free-living species than in the insecticolous forms. The chaetotaxy of the legs of the Mesostigmata has been largely ignored by acarologists, although preliminary studies by one of us (G. O. E.) indicate that the number of setae per segment, their form, and distribution are of taxonomic importance. The number of setae on various segments of the legs of species of *Macrocheles* is extremely constant (Text-fig. *2a–d*) ; the only segment showing interspecific variation is the genu of leg IV. This segment may have six or seven setae (Text-fig. 2*d* and *e*). There appears to be no definite correlation between the number of setae in the J-series (two or three) and the chaetotaxy of femur IV ; although species of the *Holocelaeno*-group which we have examined have three setae in the J-series and seven setae on femur IV. The leg setae show considerable variety in form. Those on tarsus II tend to become thickened and spine-like (Text-fig. 10). The number of setae on the various segments of the legs (excluding tarsus I) is given in the following table (Table I).

TABLE I.—Numbers of Setae on the Leg Segments of *Macrocheles* Latr.

Leg	Coxa	Trochanter	Femur	Genu	Tibia	Tarsus
I	2	5	13	11	12	—
II	2	5	11	11	10	18
III	2	5	6	7	7	18
IV	1	5	6	6/7	7	18

The nomenclature for the setae on genu IV is given in Text-fig. 2*e*.

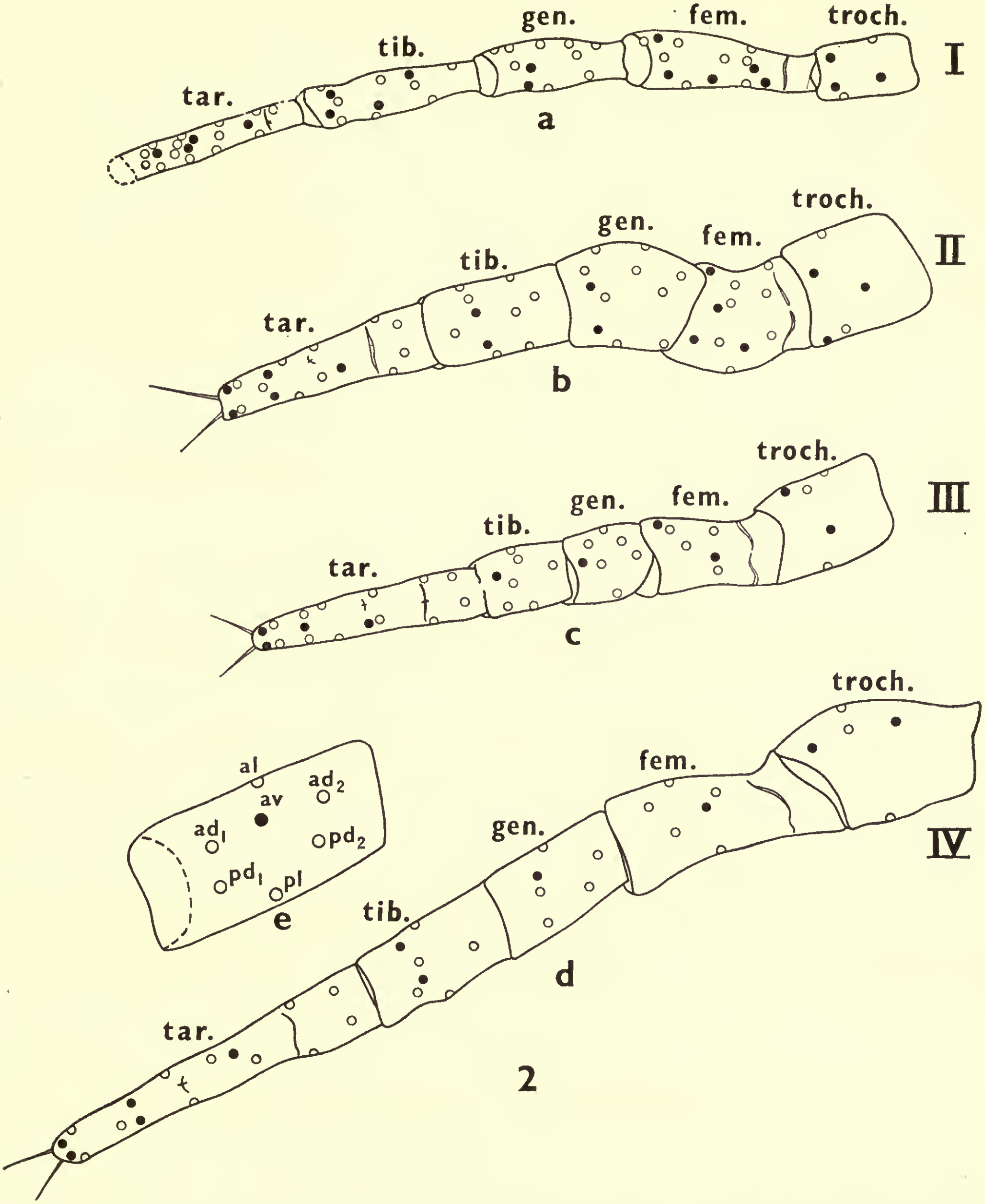
The variety of morphological characters exhibited by the insecticolous *Macrocheles* suggests the possibility of their division into supraspecific groups. Of the characters we have considered, the following three appear to be the most promising since they are readily definable and are subject to little or no intraspecific variation :

a. The number of setae in the J-series on the dorsal shield ;

b. The number of setae on genu IV ;

c. The form and length of the brush-like process of the arthrodial membrane at the base of the movable digit of the chelicera.

The relationships between the groupings obtained by using these characters singly or in combination seem to be intra- rather than intergeneric. In view of this we have considered it inadvisable at present to propose new taxa. We have, however, given these units the status of species-groups. Until a comprehensive study can be undertaken on the external morphology of the family as a whole, the weighting of the characters we have used must, of necessity, be arbitrary. The emphasis on the importance of the chaetotaxy of the dorsal shield in the definition of the species groups has practicability and not phylogeny as its basis. The forty-six species



tar.
tib.
gen.
fem.
troch.
I
a
II
b
III
c
IV
d
al
ad2
av
ad1
pd2
pd1
pl
e

2

FIG. 2*a–d*. The distribution of setae on legs I–IV of adult *Macrocheles* Latr. excluding the coxae. e, nomenclature for the setae on genu IV. The black dots denote the positions of setae occurring ventrally on the segments. ad_1, ad_2, antero-dorsal setae; al, antero-lateral seta; av, antero-ventral seta; fem., femur; gen., genu; pd_1, pd_2, postero-dorsal setae; pl, postero-lateral seta; tar., tarsus; tib., tibia; troch., trochanter.

considered in this work may be separated into the following distinct groups :

a. Cheliceral " brush " long, filamentous and extending up to or beyond the distal end of the movable digit of the chelicera (Text-fig. 136) ; dorsal shield with 29 pairs of setae[1] (Text-fig. 134) ; genu IV with seven setae *mitis*-group (p. 378)

– Cheliceral " brush " shorter, its processes never filamentous, rarely extending to the distal end of the movable digit (Text-fig. 5) ; dorsal shield with 28 or 29 pairs of setae ; genu IV with six or seven pairs of setae . . . . . b

b. Dorsal shield with 28 pairs of setae, J2 absent (Text-fig. 3) . *glaber*-group[2] (p. 332)

– Dorsal shield with 29 pairs of setae, J2 present (Text-fig. 171) *bregetovae*-group (p. 389)

GLABER–group

Macrocheles abbreviatus Berlese, 1918

Macrocheles (*Copriholaspis*) *abbreviatus* Berlese, A., 1918, *Redia* **13** : 151.

FEMALE. Dorsal shield (890μ long × 529μ wide) finely granular, reticulated, with a procurved transverse line medially, and bearing 28 pairs of setae (Text-fig. 3). The verticals, i1, are two diameters apart and slightly pilose distally ; setae r4, r5, zl, i3 and J5 are also pilose, remainder simple.

Sternal shield granular, with conspicuous undulating transverse lines in its anterior third. *L.m.t.* undulating, *l.o.p.* conspicuous (Text-fig. 4). Genital shield truncated posteriorly, granular, and with punctate ornamentation. Ventri-anal shield (289μ long × 258μ wide) granular and with recurved transverse lines. The nine setae are simple.

The chelicera is shown in Text-fig. 5. The brush-like process of the synarthrodial membrane is half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout simple setae. Tarsus II (Text-fig. 6) 187μ, tibia II 106μ.

MALE. Unknown.

DISTRIBUTION. Berlese (1918) recorded this species from *Atheucus* sp. in Italian Somaliland. The Museum collections contain five females on *Scarabaeus prodigiosus* Erichs., collected by W. E. Cutler (1924–283) at Dar-es-Salaam, Tanganyika ; and over a dozen females from a " coprid beetle ", Commonwealth Institute of Entomology No. 7766, from N. Bujishu, Uganda.

Macrocheles argentinus sp. nov.

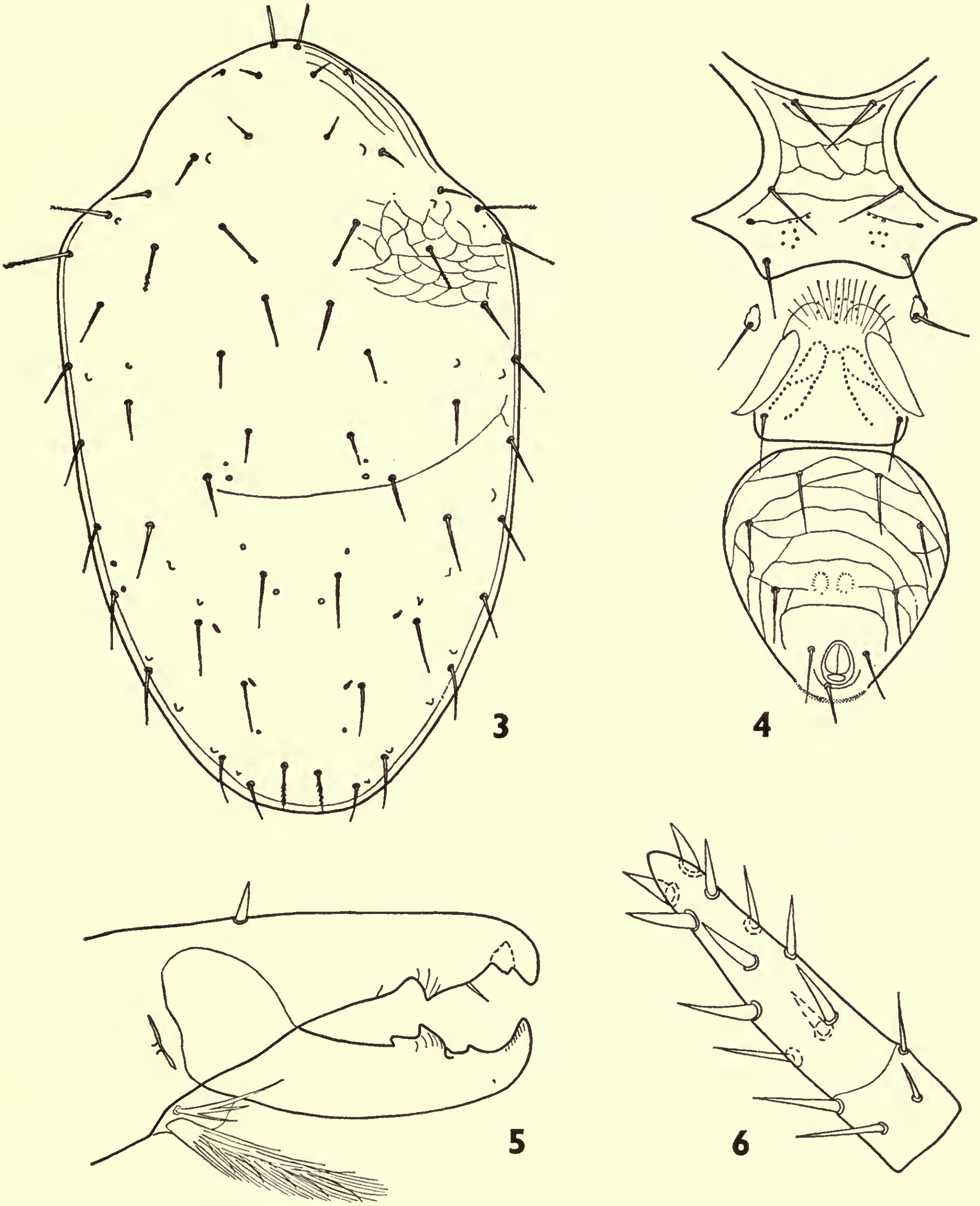
FEMALE. Dorsal shield (580μ long × 330μ wide) finely granular, entirely reticulated, and bearing 28 pairs of setae (Text-fig. 7). The verticals, i1, are thorn-like and project anteriorly, whilst J5 are short and serrated. The remaining setae are simple.

Sternal shield granular with some punctate ornamentation. *L.m.t.* undulating, incomplete medially ; *l.arc.* recurved, discontinuous ; *l.o.p.* not reaching to *l.m.t.* (Text-fig. 8). Genital shield granular, truncated posteriorly and with a strongly recurved punctate line connecting the setal bases. Ventri-anal shield (178μ long × 164μ wide) granular with only faint traces of reticulation. The nine setae are simple.

---

[1] Krantz (1962) states that the genus *Holocelaeno* has 28 pairs of setae on the dorsal shield. All the species of this group we have examined have 29 pairs.

[2] We have not considered the *Macrocheles glaber*-complex in this work since intensive laboratory studies on this " species " are being undertaken by Dr. Filipponi and Dr. Pegazzano.

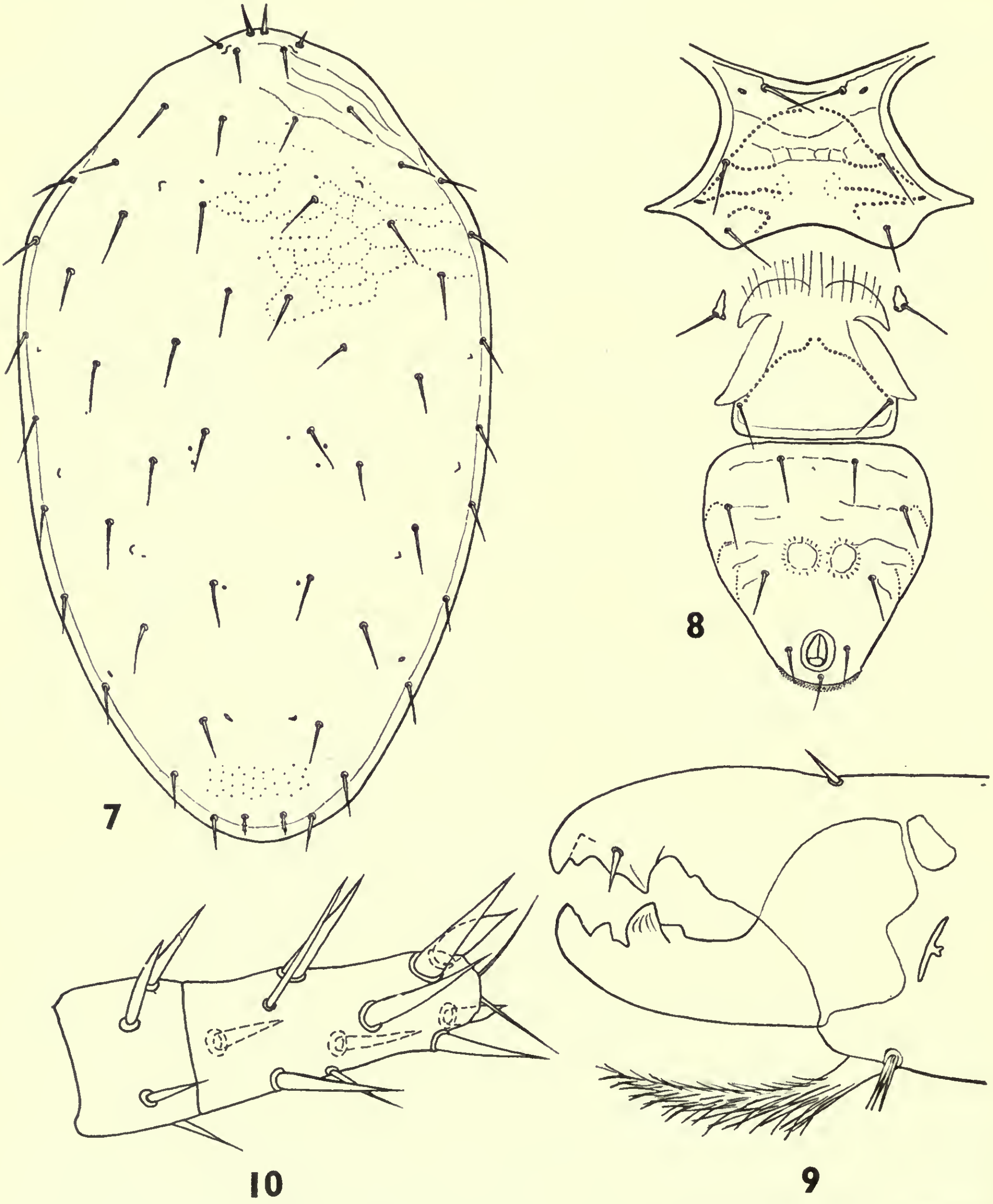


FIGS. 3–6. *Macrocheles abbreviatus* Berlese, female. Fig. 3, dorsal shield. Fig. 4, ventral shields. Fig. 5, chelicera. Fig. 6, tarsus II.

The chelicera is shown in Text-fig. 9. The brush-like process of the synarthrodial membrane is three-quarters the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout simple setae. Tarsus II 101μ (Text-fig. 10), tibia II 73μ.

MALE. Unknown.



FIGS. 7–10. *Macrocheles argentinus* sp. nov., female. Fig. 7, dorsal shield. Fig. 8, ventral shields. Fig. 9, chelicera. Fig. 10, tarsus II.

LOCALITIES. The holotype female (1961.7.14.264) and ten paratypes (1961.7.14.265–274) on *Eudinopus dytiscoides* Schreiberg, collected by G. E. Bryant (1919–147) at Villa Valeria, Argentina ; and one paratype (1961.7.14.275) from the same species of beetle in the Nevinson collection (1918–14) labelled " S. America ".

Macrocheles bacchusi sp. nov.

FEMALE. Dorsal shield (722μ long × 415μ wide) with ornamentation consisting of fine dotted reticulations and bearing 28 pairs of setae (Text-fig. 11). The majority of the dorsal setae are finely pilose distally, but setae r1, i5, s5, J3 and Z3 are simple. The verticals, i1, are almost two diameters of their bases apart.

Sternal shield granular with symmetrical punctate ornamentation. *Liniae* concealed in the ornamentation (Text-fig. 12). Genital shield granular, truncated posteriorly, and with punctate ornamentation. Ventri-anal shield (237μ long × 206μ wide) pear-shaped in the figured specimen (the holotype), but variable in outline, granular, and with transverse punctate lines. The nine ventri-anal setae are simple.

The chelicera is shown in Text-fig. 13. The synarthrodial brush of setae is half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout setae all of which are pilose, or bipectinate, distally. Tarsus II (Text-fig. 14) 152μ, tibia II 86μ.

MALE. Unknown.

LOCALITIES. The holotype female (1961.7.14.276) and three paratypes (1961.7.14.277–279) on *Circellium bacchus* Fabr., collected by Burchell (1110b) in " Africa " ; and one paratype (1961.7.14.280) on *Macroderes greeni* Kirby, collected by R. E. Turner (1928–421) at Worcester, Cape of Good Hope.

Macrocheles baramensis sp. nov.

FEMALE. Dorsal shield (825μ long × 540μ wide) granular, covered by fine reticulations and bearing 28 pairs of setae (Text-fig. 15). The vertical setae, i1, have their bases touching and are pilose in their distal halves. Setae i4, i5, z2, z3 and J3 are simple, all other dorsal setae are finely bipectinate in their distal halves.

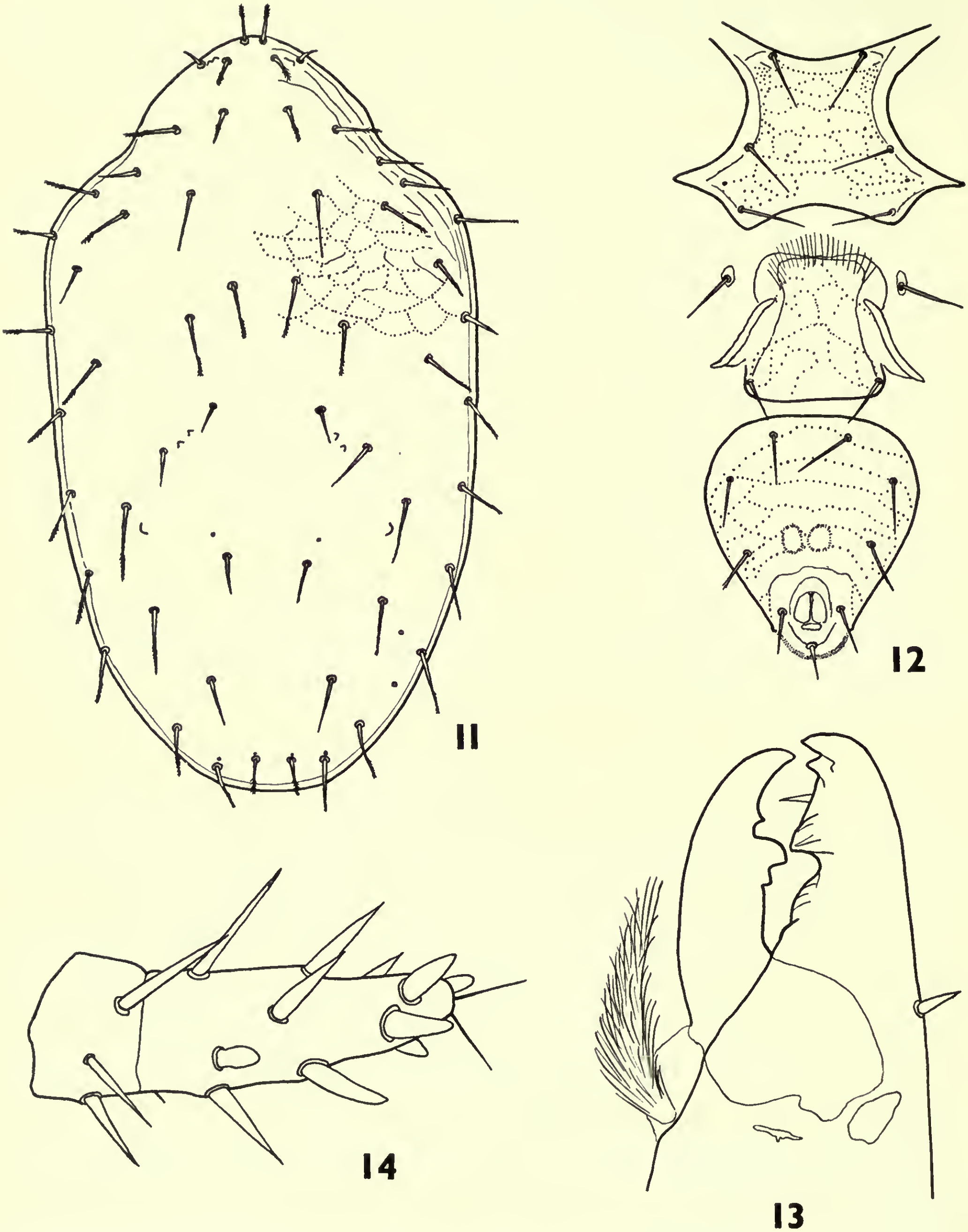
Sternal shield granular, with faint traces of linear ornamentation. *L.m.t.* undulating, slightly procurved, *l.arc.* incomplete, *l.o.p.* conspicuous (Text-fig. 16). Genital shield granular. Ventri-anal shield (280μ long × 205μ wide) with conspicuous transverse lines ; all setae simple except for the finely-pilose post-anal.

The chelicera is shown in Text-fig. 17. The brush-like process of the synarthrodial membrane is two-thirds the length of the movable digit. Six rows of deutosternal teeth.

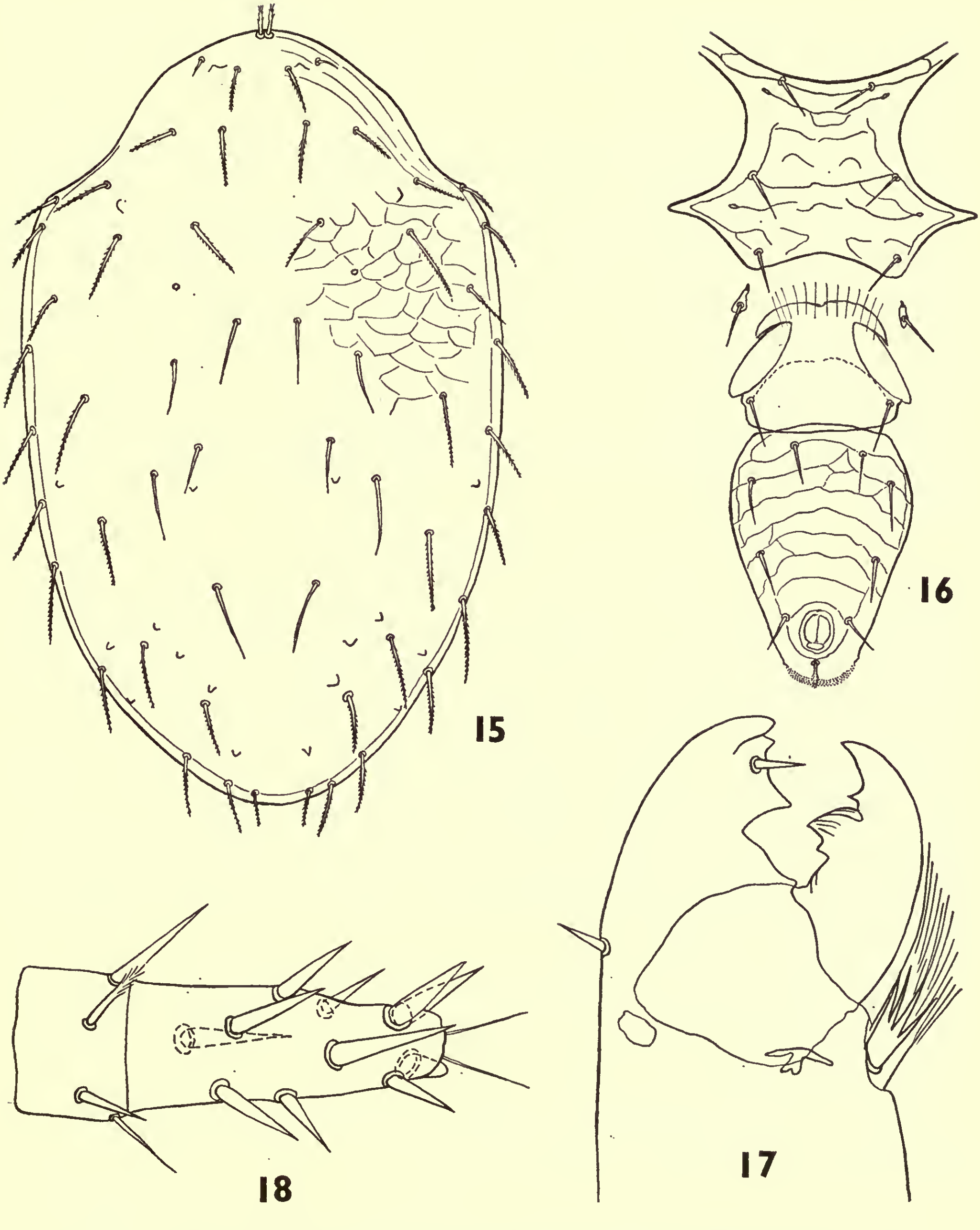
Genu IV with six stout setae all of which are strongly pilose. Tarsus II (Text-fig. 18) 194μ, tibia II 126μ.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.251) and three paratypes (1961.7.14.252–254) on *Gymnopleurus maurus* Sharp, collected by A. Everett (1892–8) at Baram, NW. Borneo.



FIGS. 11–14. *Macrocheles bacchusi* sp. nov., female. Fig. 11, dorsal shield. Fig. 12, ventral shields. Fig. 13, chelicera. Fig. 14, tarsus II.



FIGS. 15–18. *Macrocheles baramensis* sp. nov., female. Fig. 15, dorsal shield. Fig. 16, ventral shields. Fig. 17, chelicera. Fig. 18, tarsus II.

Macrocheles boxi sp. nov.

FEMALE. Dorsal shield (560µ long × 340µ wide) finely granular and with faint reticulations, and bearing 28 pairs of setae (Text-fig. 19). All setae are simple with the exception of J5 which are finely serrated. The thorn-like verticals are about one diameter apart.

Sternal shield granular. *L.m.t.* slightly procurved, *l.arc.* recurved, discontinuous anteriorly, *l.o.p.* extending almost to the centre of the sternal shield (Text-fig. 20). Genital shield small, granular, and truncated posteriorly. Ventri-anal shield (165µ long × 145µ wide) finely granular, with faint transverse lines and nine simple setae.

The chelicera is shown in Text-fig. 21. The brush of setae on the synarthrodial membrane is about half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six simple setae. Chaetotaxy of legs simple. Tarsus II 104µ (Text-fig. 22), tibia II 75µ.

MALE. Unknown.

LOCALITY. The holotype female (1916.7.14.56) and one paratype (1961.7.14.57) on *Canthon principalis* Burm. collected by H. E. Box (1930–238) at Tucuman, Argentina.

Macrocheles browningi sp. nov.

FEMALE. Dorsal shield (1,040µ long × 640µ wide) with a very characteristic pattern of punctations and reticulations, and with a procurved transverse line medially, and bearing 28 pairs of dorsal setae (Text-fig. 23). The vertical setae, i1, are broad and elliptical with finely pectinate edges. Setae i3, i4, i5, z1, z2, z3, s5 s6, J3, Z1, Z2 and Z3 are simple, the remaining setae are finely pilose.

Sternal shield large, very characteristically ornamented with areolations and lines. *L.m.t.* undulating, *l.arc.* strongly recurved, discontinuous anteriorly, *l.ang.* and *l.o.p.* formed by the ornamentation (Text-fig. 24). Genital shield broad, truncated posteriorly and with a symmetrical punctate design. Ventri-anal shield (340µ long × 435µ wide) truncated anteriorly, ornamented with transverse areolate lines and strongly-punctate areas posterolaterally. The post-anal seta is finely pilose, the remaining eight are simple.

The chelicera is shown in Text-fig. 25. The synarthrodial brush of setae is about half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout pilose setae. Tarsus II 205µ (Text-fig. 26), tibia II 120µ.

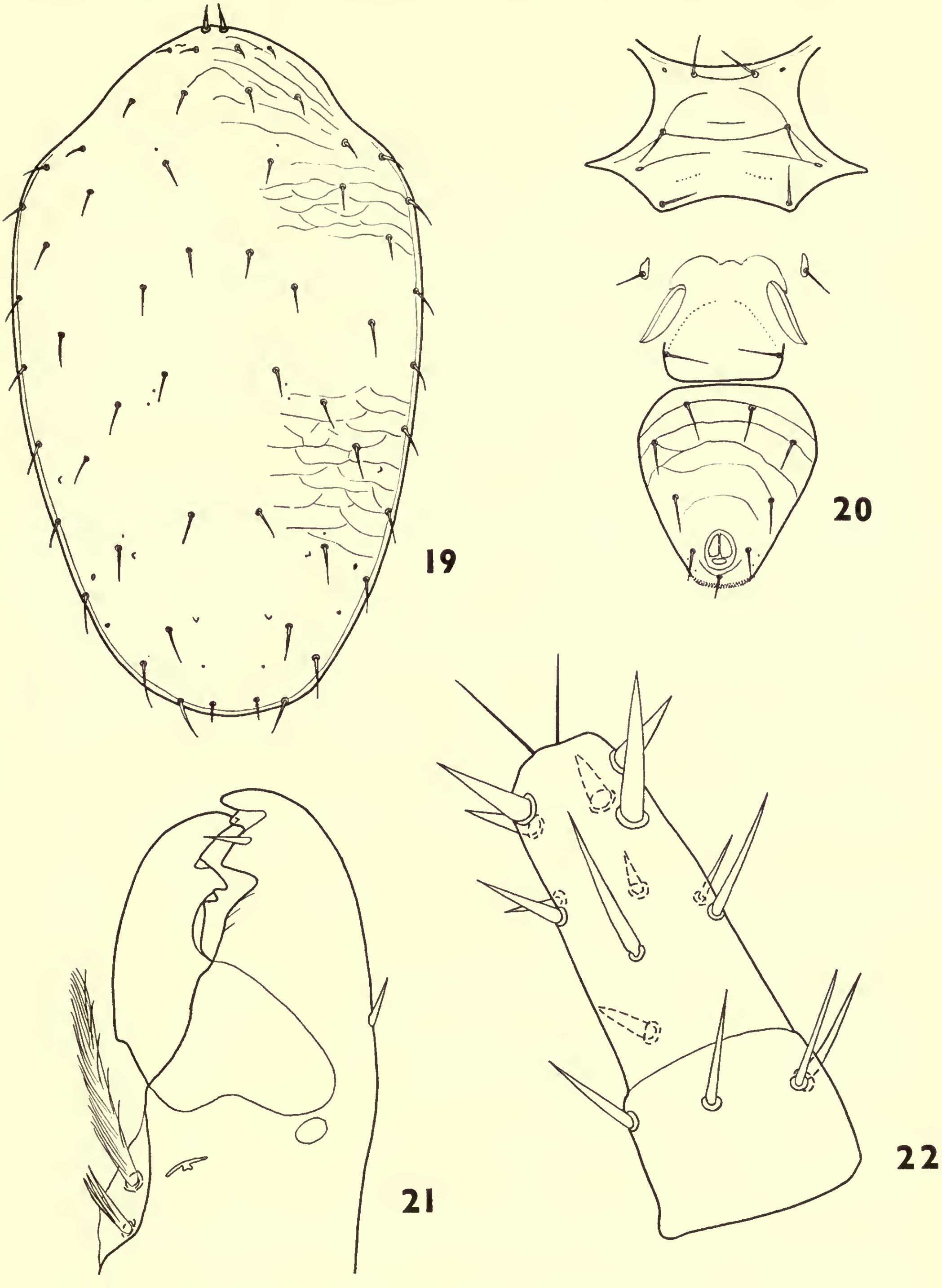
MALE. Unknown.

LOCALITY. A single female (1961.7.14.147) on *Eurysternus deplanatus* Germar in the Fry collection (1905–100), from Rio de Janeiro, Brazil.

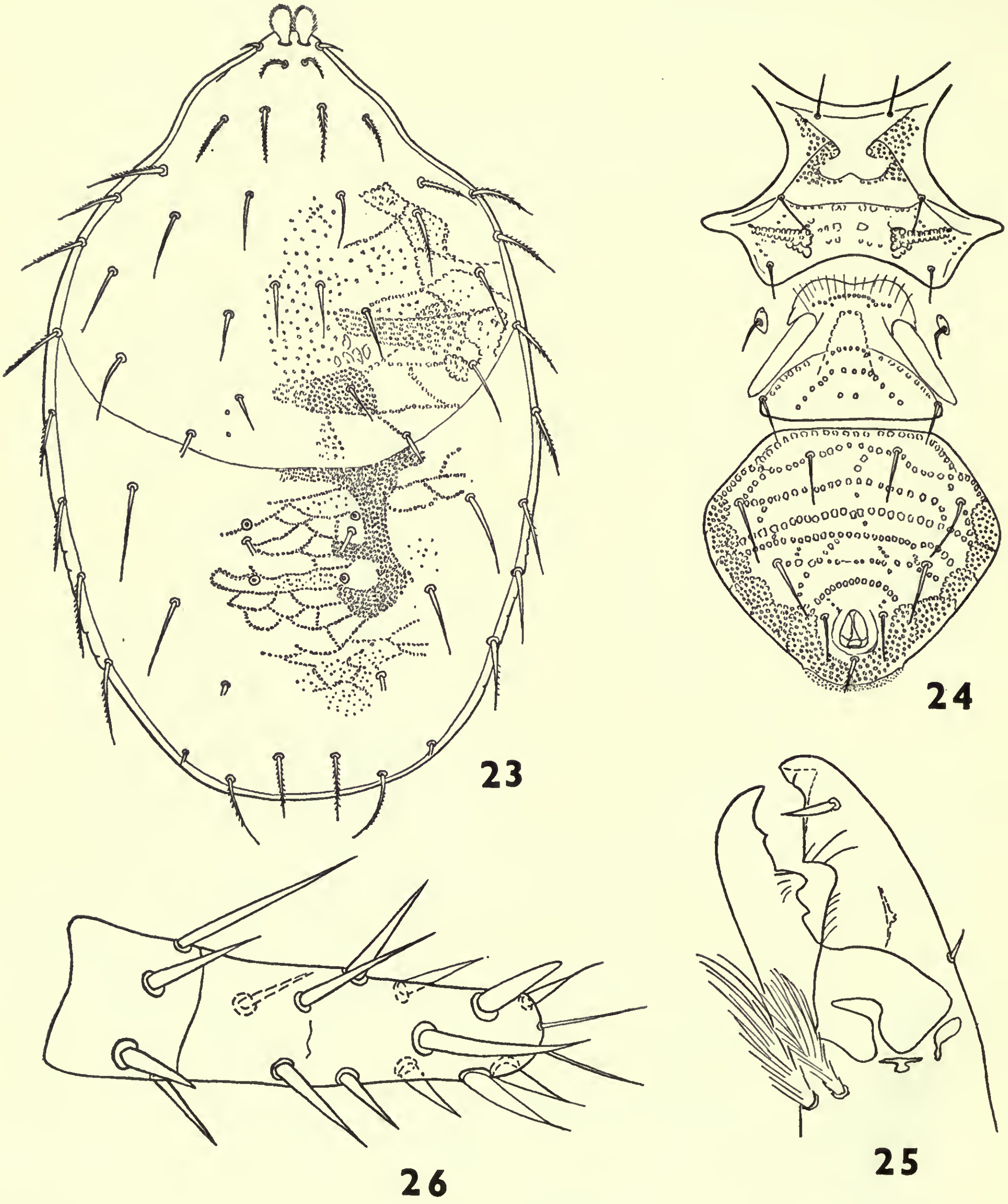
This species is named after Mr. E. Browning.

Macrocheles bryanti sp. nov.

FEMALE. Dorsal shield (930µ long × 515µ wide) with a fine punctate ornamentation and bearing 28 pairs of setae (Text-fig. 27). The verticals, i1, are flat and



FIGS. 19–22. *Macrocheles boxi* sp. nov., female. Fig. 19, dorsal shield. Fig. 20, ventral shields. Fig. 21, chelicera. Fig. 22, tarsus II.



Figs. 23–26. *Macrocheles browningi* sp. nov., female. Fig. 23, dorsal shield. Fig. 24, ventral shields. Fig. 25, chelicera. Fig. 26, tarsus II.

elliptical with strongly dentate margins; r1 are the shortest setae, and all are finely bipectinate. J2 absent.

Sternal shield with punctate areas and little or no reticulation. Structural lines inconspicuous and rudimentary, represented mainly by the limits of the porose areas (Text-fig. 28). Genital shield very shallow, broad, truncated posteriorly and with little ornamentation. Ventri-anal shield (310μ long × 260μ wide) with punctate transverse lines and a porose area on each side of the anus. The nine setae are simple.

The chelicera is shown in Text-fig. 29. The brush of setae on the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with seven pilose setae. Tarsus II 205μ (Text-fig. 30), tibia II 145μ.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.125) and two paratypes (1961.7.14.126–127) on *Eurysternus calligrammus* Dalm. collected by G. E. Bryant (1919–147) near Santos, Ihla Santo Amaro, Brazil.

Macrocheles carteri sp. nov.

FEMALE. Dorsal shield (670μ long × 400μ wide) with fine reticulations covering the entire surface, and bearing 28 pairs of setae (Text-fig. 31). The verticles, i1, are very finely pilose distally and their bases are almost contiguous. The remaining setae are simple.

Sternal shield granular with punctate ornamentation. *Liniae* not discernible (Text-fig. 32). Genital shield short, granular, truncated posteriorly and with punctate ornamentation. Ventri-anal shield (225μ long × 195μ wide) finely granular and with punctate transverse lines.

The chelicera is shown in Text-fig. 33. The brush of setae on the synarthrodial membrane is over half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout setae of which *av* is palmate distally and the remainder are simple. Tarsus II 139μ (Text-fig. 34), tibia II 88μ.

MALE. Unknown.

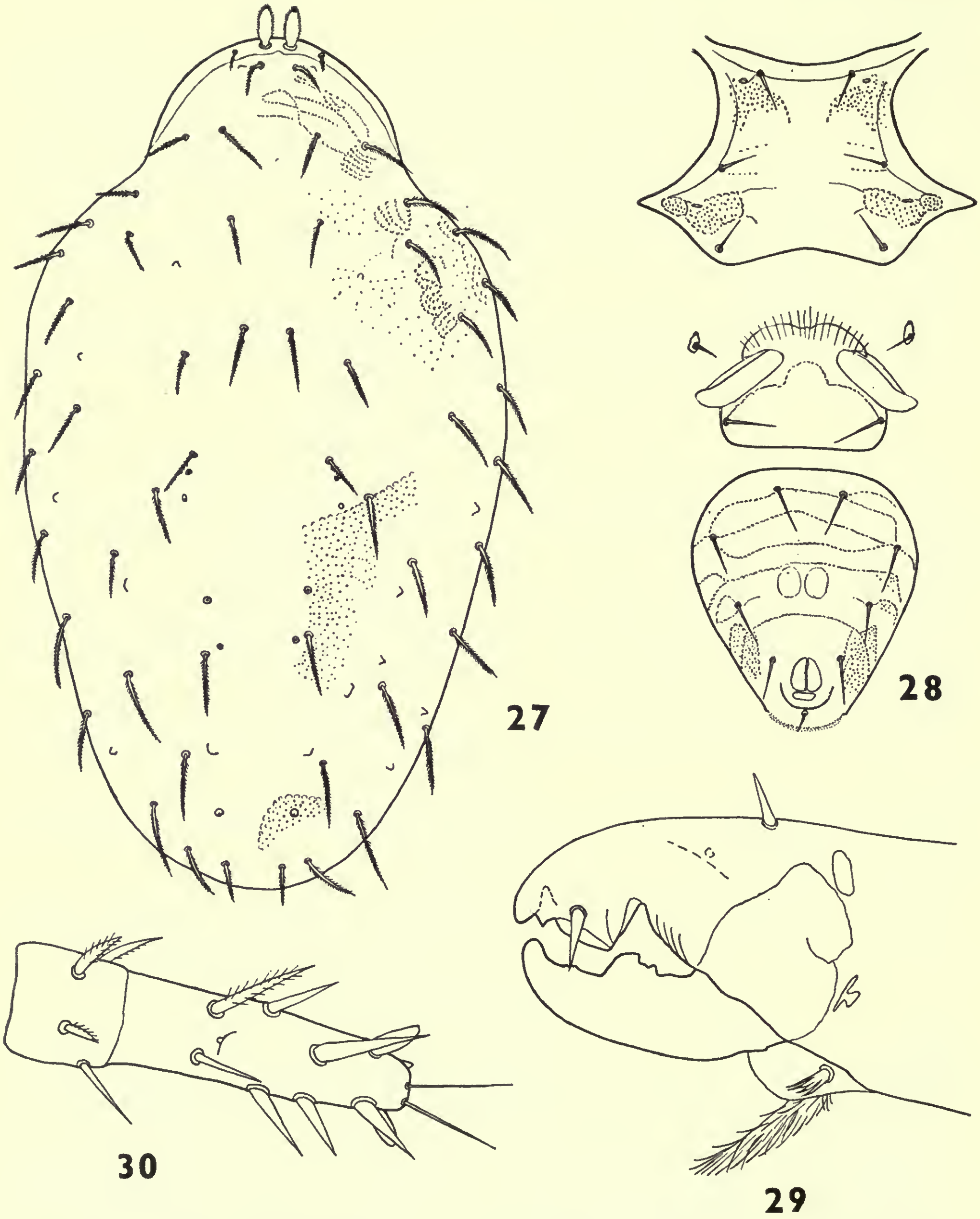
LOCALITY. A single female (1961.7.14.55) on *Phanaeus imperator* Chevr. collected by G. S. Carter (1928–50) at Nanahua in the Paraguayan Chaco.

Macrocheles ceylonicus sp. nov.

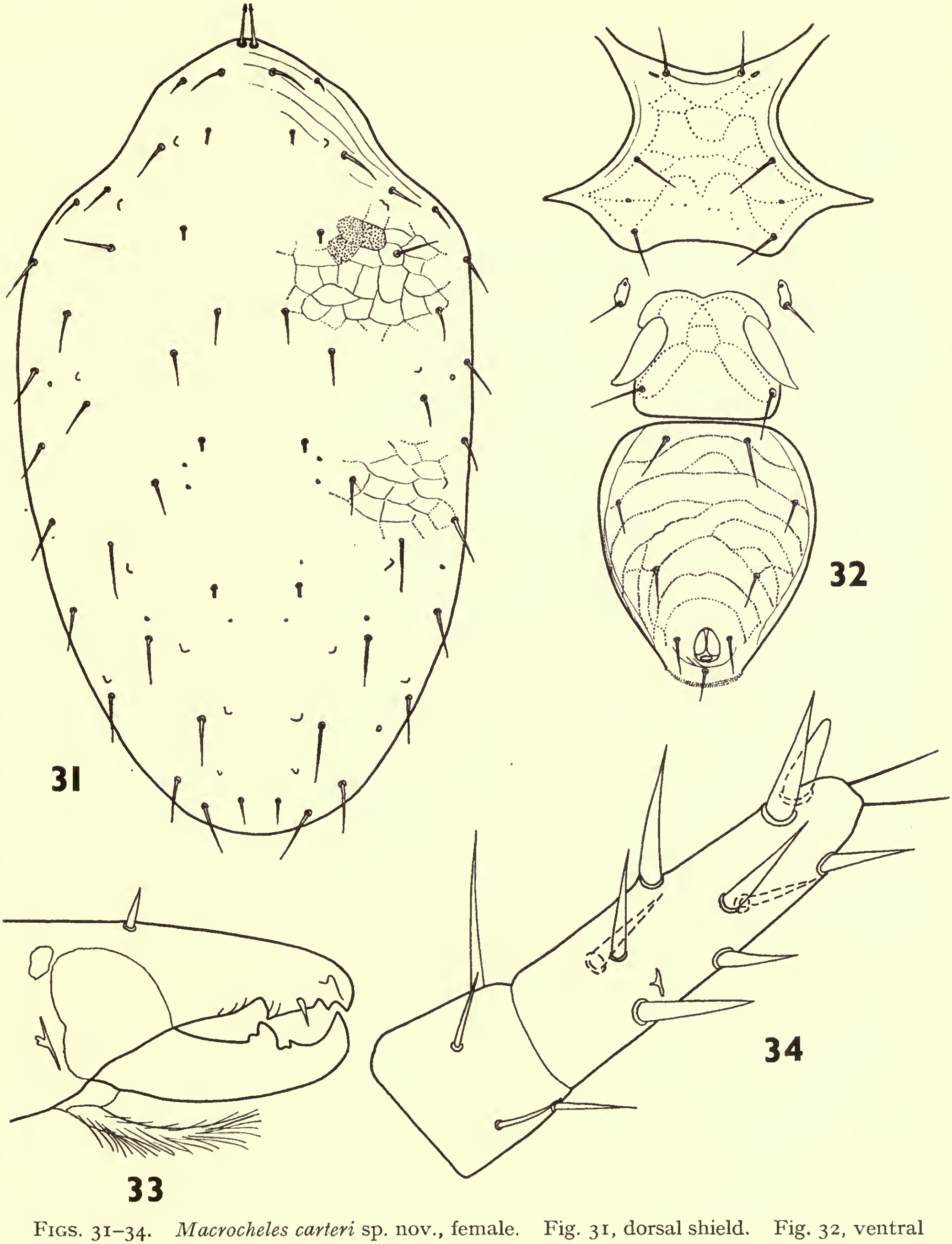
FEMALE. Dorsal shield (726–803μ long × 429–473μ wide) finely granular, covered with a dotted reticulated pattern and bearing 28 pairs of setae (Text-fig. 35). Vertical setae, i1, and also r4, z1, s5 and J5 slightly pilose, remainder simple.

Sternal shield very characteristically ornamented with small elongate depressions following to a certain degree the *liniae*. *L.m.t.* undulating, *l.arc.* strongly recurved (Text-fig. 36). Genital shield granular, with punctate lines. Ventri-anal shield (231–264μ long × 182–198μ wide) with ornamentation of transverse intersecting lines of depressions. The nine ventri-anal setae are simple.

The chelicera is shown in Text-fig. 37. The brush-like process of the synarthrodial membrane is half the length of the movable digit. Six rows of deutosternal teeth.



FIGS. 27–30. *Macrocheles bryanti* sp. nov., female. Fig. 27, dorsal shield. Fig. 28, ventral shields. Fig. 29, chelicera. Fig. 30, tarsus II.



FIGS. 31–34. *Macrocheles carteri* sp. nov., female. Fig. 31, dorsal shield. Fig. 32, ventral shields. Fig. 33, chelicera. Fig. 34, tarsus II.

Genu IV with six setae all of which are simple. Tarsus II 164μ (Text-fig. 38), tibia II 113μ.

MALE. Unknown.

LOCALITIES. The holotype female (1961.7.14.536) and two paratypes (1961.7.14.537–538) on *Scarabaeus erichsoni* Harold, collected by J. J. Walker (1890–80) at Colombo, Ceylon; and six paratypes (1961.7.14.539–544) also on *Scarabaeus erichsoni* in the Vigors collection (1859–57) from Madras, India.

Macrocheles cognatus Berlese, 1918

Macrocheles (*Coprholaspis*) *cognatus* Berlese, A., 1918, *Redia* **13** : 159.

FEMALE. Dorsal shield (630μ long × 340μ wide) granular, with faint reticulations and bearing 28 pairs of setae (Text-fig. 39). With the exception of J5, which are finely bipectinate, all setae are simple. Verticals, i1, contiguous and thorn-like. A faint procurved line extends across the dorsal shield medially.

Sternal shield with conspicuous punctate ornamentation. *L.m.t.* slightly undulating, *l.arc.* strongly recurved, discontinuous anteriorly, *l.o.p.* extending across the shield and almost parallel to *l.m.t.* (Text-fig. 40). Genital shield granular, truncated posteriorly. Ventri-anal shield (175μ long × 165μ wide) ovoid, granular, with punctate transverse lines and bearing nine simple setae.

The chelicera is shown in Text-fig. 41. The brush of setae on the synarthrodial membrane is three-quarters the length of the movable digit.

Genu IV with six simple setae. Tarsus II 116μ (Text-fig. 42), tibia II 76μ. Femur, genu and tibia of legs II–IV with blunt tooth-like projections basally.

MALE. Unknown.

DISTRIBUTION. Berlese (1918) recorded this species from *Phanaeus* sp. at La Plata, Argentina, and Parà, Brazil. The Museum collections contain 19 females: 10 on *Phanaeus imperator* Chevr., collected by O. W. Thomas (1904–148) in Argentina; seven on *Phanaeus bonariensis* Gory, collected by E. G. Kent (1925–262) at Asuncion, Paraguay; and two on *Phanaeus lancifer* L., labelled " S. America ".

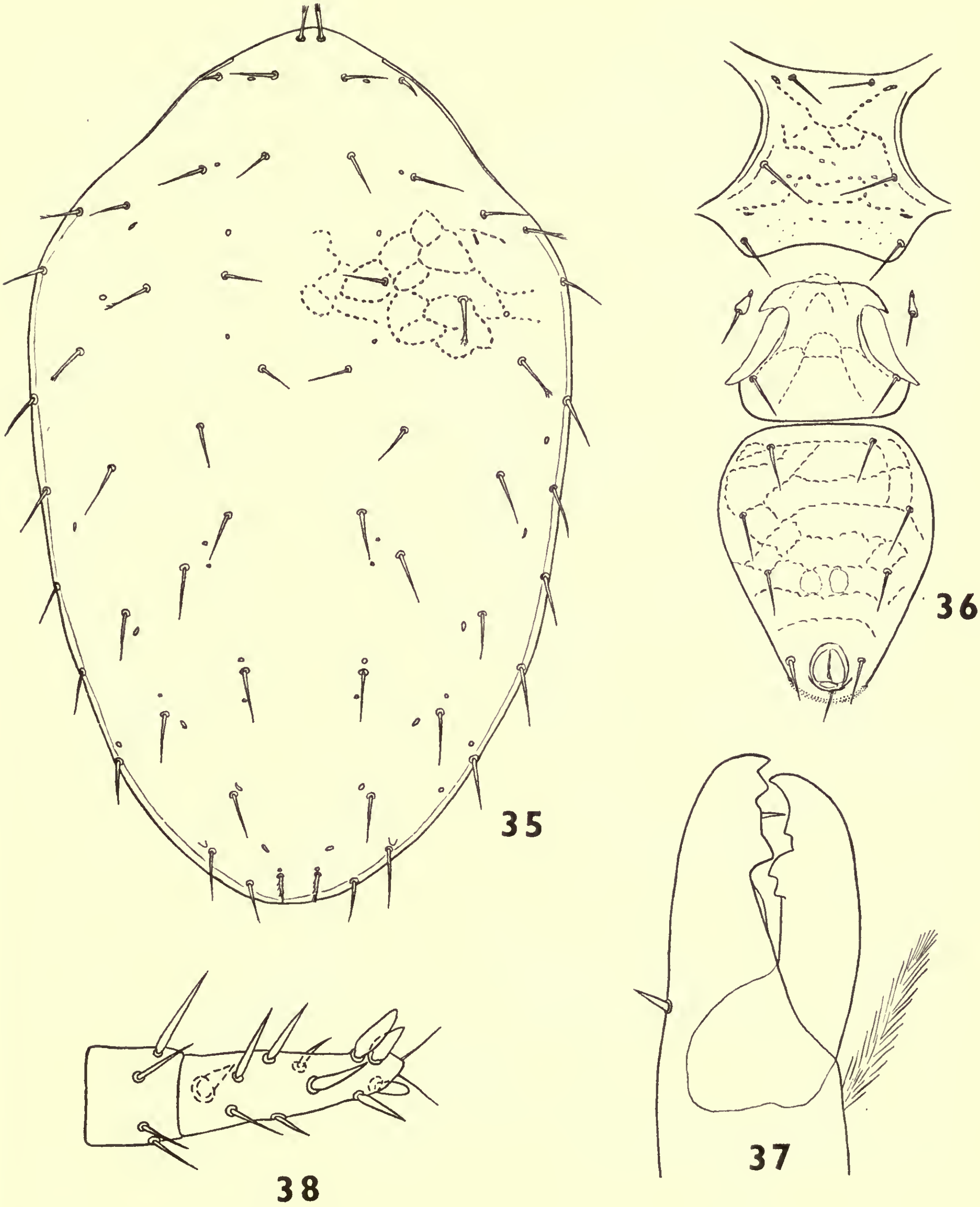
This species is superficially like *M. vernalis* Berl. in the sculpturing of the sternal shield and chaetotaxy of the dorsal shield. It differs in the size of the ventri-anal shield and in the presence of tooth-like projections from the femur, genu and tibia of legs II–IV.

Macrocheles dimidiatus Berlese, 1918

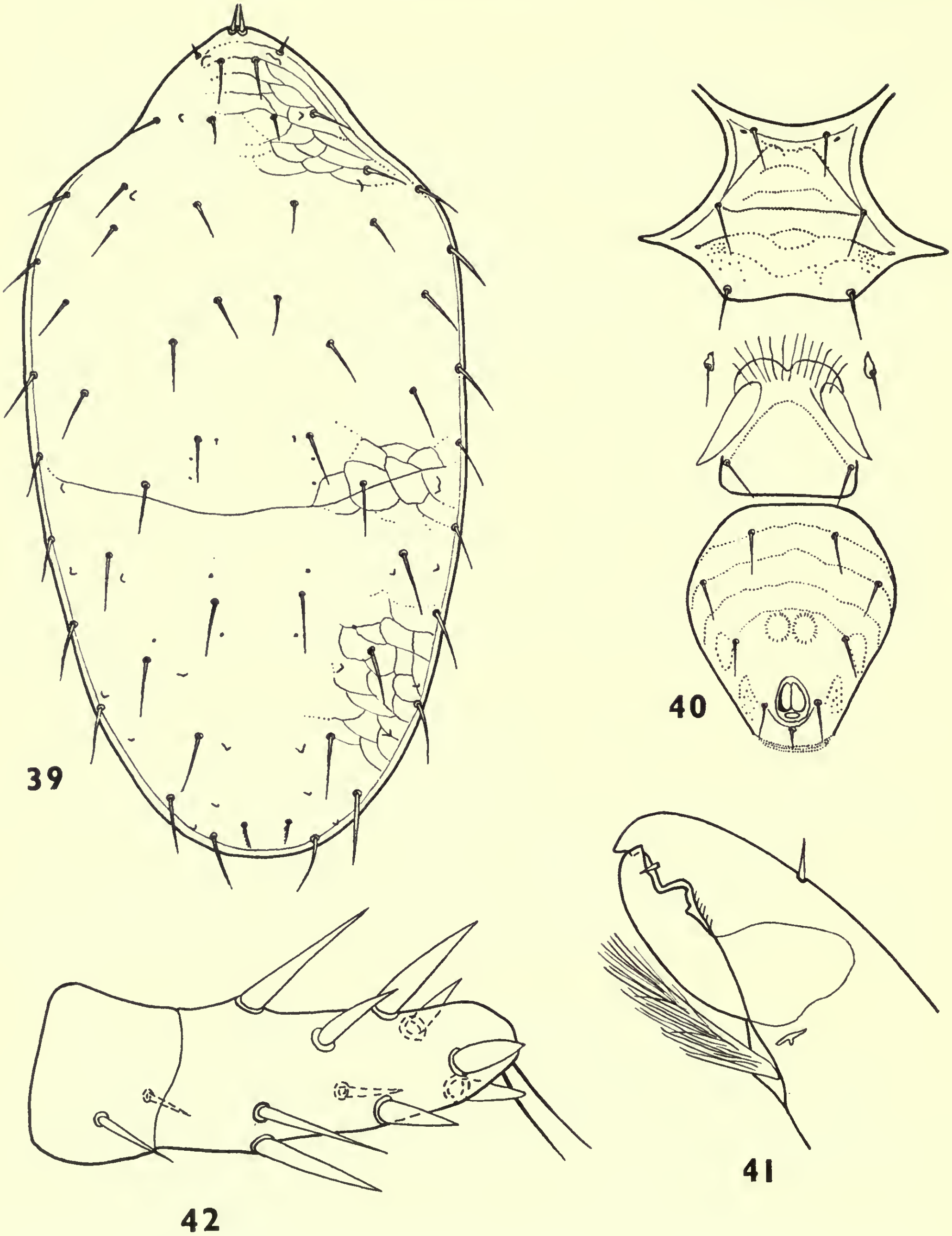
Macrocheles (*Coprholaspis*) *dimidiatus* Berlese, A., 1918, *Redia* **13** : 163.

FEMALE. Dorsal shield (800–880μ long × 466–570μ wide) granular, with areas of reticulations and areolations, and with a strongly-recurved line medially and bearing 28 pairs of setae (Text-fig. 43). Setae i1, the verticals, are broad and leaf-like with finely-dentate margins. Setae z2, i5 and J3 are simple; all remaining setae are noticeably bipectinate.

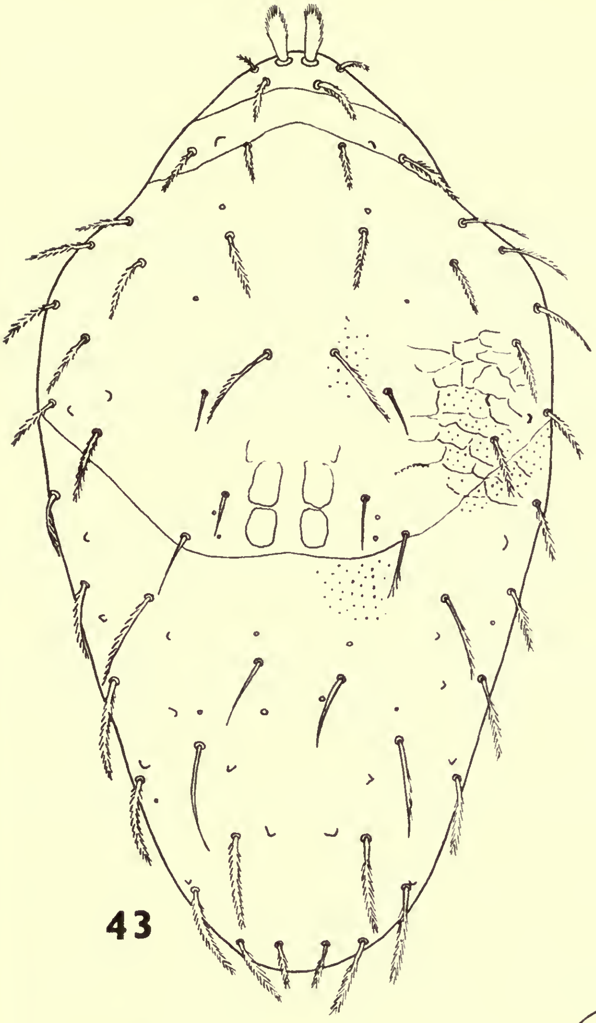
Sternal shield granular, *areae punctatae* conspicuous. *L.m.t.* slightly recurved, *l.arc.* strongly recurved, discontinuous medially (Text-fig. 44). Genital shield broad, truncated posteriorly and finely granular. Ventri-anal shield (242μ long × 173μ



Figs. 35–38. *Macrocheles ceylonicus* sp. nov., female. Fig. 35, dorsal shield. Fig. 36, ventral shields. Fig. 37, chelicera. Fig. 38, tarsus II.



FIGS. 39–42. *Macrocheles cognatus* Berlese, female. Fig. 39, dorsal shield. Fig. 40, ventral shields. Fig. 41, chelicera. Fig. 42, tarsus II.



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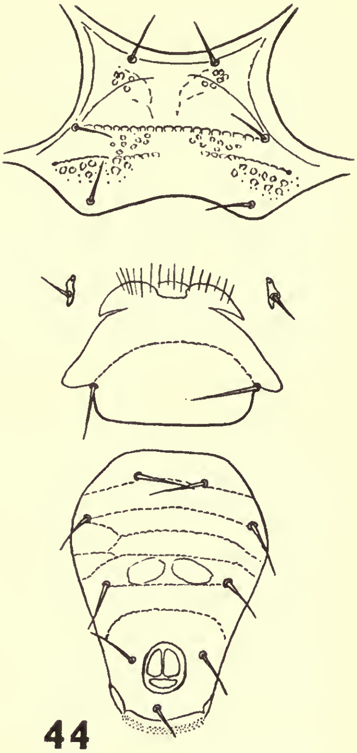

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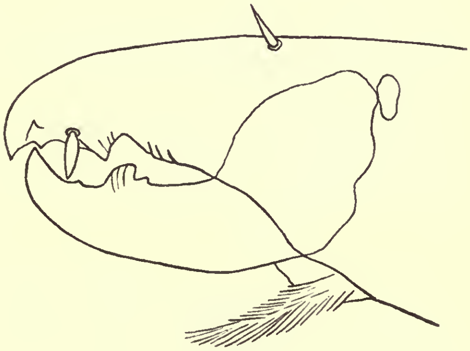

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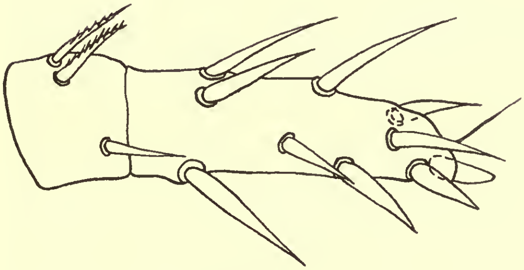

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Figs. 43–46. *Macrocheles dimidiatus* Berlese, female. Fig. 43, dorsal shield. Fig. 44, ventral shields. Fig. 45, chelicera. Fig. 46, tarsus II.

wide) truncated anteriorly, granular and with transverse punctate lines. All nine ventri-anal setae are simple.

The chelicera is shown in Text-fig. 45. The brush-like process of the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with six stout setae all of which are strongly pilose. Tarsus II 169μ (Text-fig. 46), tibia II 100μ.

MALE. Unknown.

DISTRIBUTION. Berlese (1918) described this species from many examples on *Phanaeus splendidulus* Fabr. and other *Phanaeus* spp., and on *Bombus* sp. at La Plata and Buenos Aires, Argentina. The Museum collections contain females from *Phanaeus amythaon* Harold at Jalisco, Guadalajara, Mexico; from *Phanaeus splendidulus* nr. Santos, Ilha Santo Amara, Brazil; from *Phanaeus faunus* Fabr. in the Forest Santarem, Lower Amazons; from *Phanaeus ensifer* Germ. at Nanahua, Paraguayan Chaco; and from *Phanaeus carnifex* L. at Deer Lodge, Tennessee.

Macrocheles distanti sp. nov.

FEMALE. Dorsal shield (671–748μ long × 385–451μ wide) granular, ornamentation of faint reticulations and bearing 28 pairs of setae (Text-fig. 47). The majority of the dorsal setae are finely pectinate distally but the following are simple: r1, s1, s5, i4, i5, z2, z3 and J3.

Sternal shield granular with punctate *liniae*. *L.m.t.* irregular, *l.o.p.* almost horizontal, continuous (Text-fig. 48). Genital shield granular. Ventri-anal shield (198–242μ long × 165–212μ wide) variable in outline, granular and with punctate transverse lines. All nine setae are simple.

The chelicera is shown in Text-fig. 49. The brush-like process of the synarthrodial membrane is a little over half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout simple setae. Tarsus II 167μ (Text-fig. 50), tibia II 118μ.

MALE. Unknown.

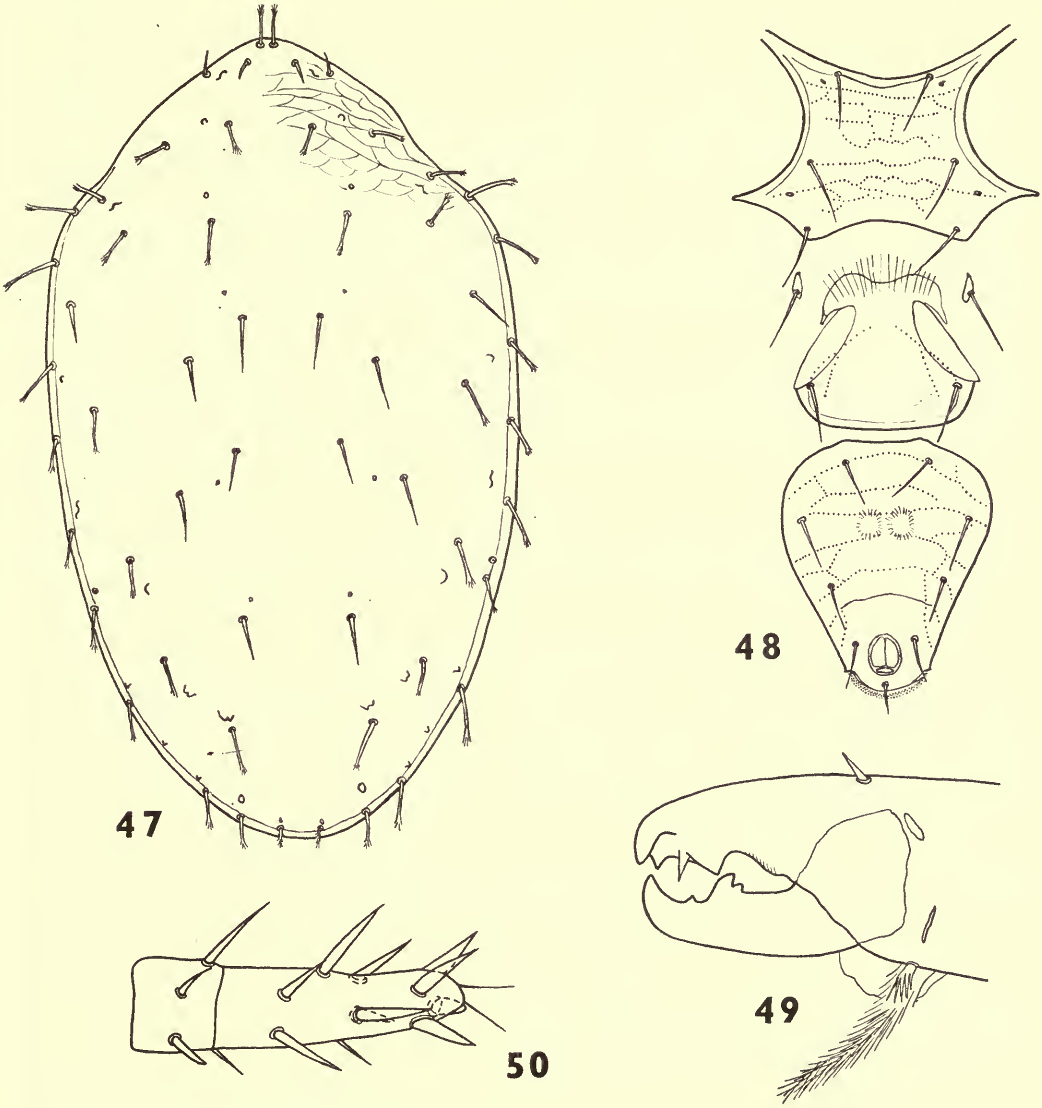
LOCALITIES. The holotype female (1961.7.14.410) and seven paratypes (1961.7.14.411–417) on *Scarabaeus bonellii* McLeay, collected by Miss A. Mackie (1948–528) at Nieuwoudtville, Cape Province; six paratypes (1961.7.14.418–423) also from *Scarabaeus bonellii*, collected by W. L. Distant (1911–383) at Cape Town; four paratypes (1961.7.14.425–428) on *Circellium bacchus* Fabr., collected by Distant at Brak Kloof Farm, Transvaal; and one paratype (1961.7.14.424) on *Circellium bacchus* in the Fry collection (1905–100) from Grahamstown, Cape Province.

Macrocheles inornatus sp. nov.

FEMALE. Dorsal shield (515μ long × 330μ wide) granular with fine reticulations only around the margin, and bearing 28 pairs of setae (Text-fig. 51). All setae are simple; the verticals, i1, are well separated.

Sternal shield granular. *L.m.t.* absent, *l.arc.* recurved, discontinuous medially (Text-fig. 52). Genital shield granular, severely truncated posteriorly. Ventri-anal shield (175μ long × 139μ wide) devoid of ornamentation.

The chelicera is shown in Text-fig. 53. The brush-like process of the synarthrodial membrane is three-quarters the length of the movable digit. Six rows of deutosternal teeth.

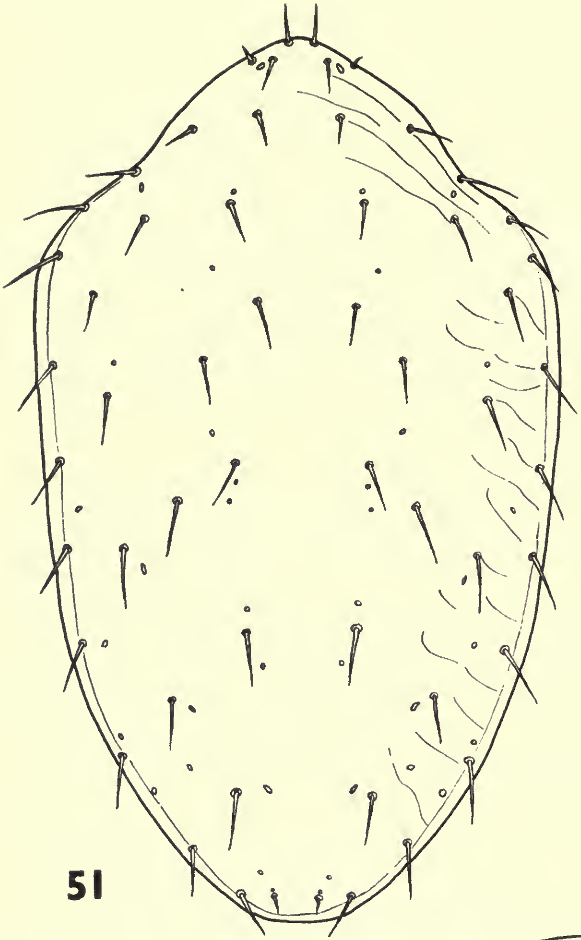


FIGS. 47–50. *Macrocheles distanti* sp. nov., female. Fig. 47, dorsal shield. Fig. 48, ventral shields. Fig. 49, chelicera. Fig. 50, tarsus II.

Genu IV with six slender simple setae. Chaetotaxy of legs simple.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.367) and one paratype (1961.7.14.368) on *Anomiopsis heteroclytum* Blanch., collected by K. J. Hayward (1933–333) at



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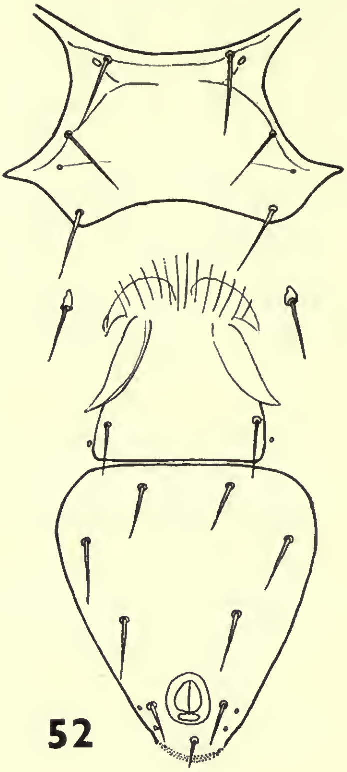

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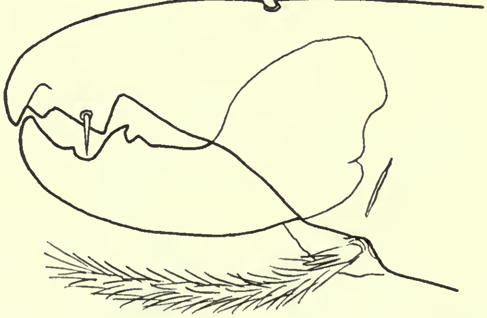

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Figs. 51–53. *Macrocheles inornatus* sp. nov., female. Fig. 51, dorsal shield. Fig. 52, ventral shields. Fig. 53, chelicera.

Patquia, La Rioja Province, Argentina; and six paratypes (1961.7.14.369–374) on *Anomiopsis bilobum* Burm., collected by Antonio Martinez (1946–164) at Tinogasta, Catamarca, Argentina.

Macrocheles japonicus sp. nov.

FEMALE. Dorsal shield (743μ long × 435μ wide) finely granular, with faint reticulations and bearing 28 pairs of setae (Text-fig. 54). The majority of the dorsal setae are very finely pilose in their distal halves, but the following are simple: r1, s1, i4, i5, z2 and J3. The verticals, i1, are contiguous. A faint procurved line extends across the dorsal shield medially.

Sternal shield with faint punctate ornamentation. *L.m.t.* slightly procurved, *l.o.p.* short (Text-fig. 55). Genital shield broad and granular, truncated posteriorly. Ventri-anal shield (268μ long × 227μ wide) with fine punctate transverse lines. All setae short and simple.

The chelicera is shown in Text-fig. 56. The brush-like process of the synarthrodial membrane is half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six short stout setae all of which are pectinate distally. Tarsus II (Text-fig. 57) 159μ, tibia II 123μ.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.257) and four paratypes (1961.7.14.258–261) on *Gymnopleurus sinuatus* Oliv., collected by G. Lewis (1910–320) in Japan.

Macrocheles krantzi sp. nov.

FEMALE. Dorsal shield (530μ long × 290μ wide) with very faint reticulations and bearing 28 pairs of short slender simple setae (Text-fig. 58).

Sternal shield granular with *liniae* short and punctate (Text-fig. 59). Genital shield granular, short and truncated posteriorly. Ventri-anal shield (180μ long × 130μ wide) ovoid, truncated posteriorly, and with transverse reticulation. The nine setae are simple.

The chelicera is shown in Text-fig. 60. The brush-like process of the synarthrodial membrane is very short. Six rows of deutosternal teeth.

Genu IV with six simple setae. Tarsus II 93μ (Text-fig. 61), tibia II 82μ.

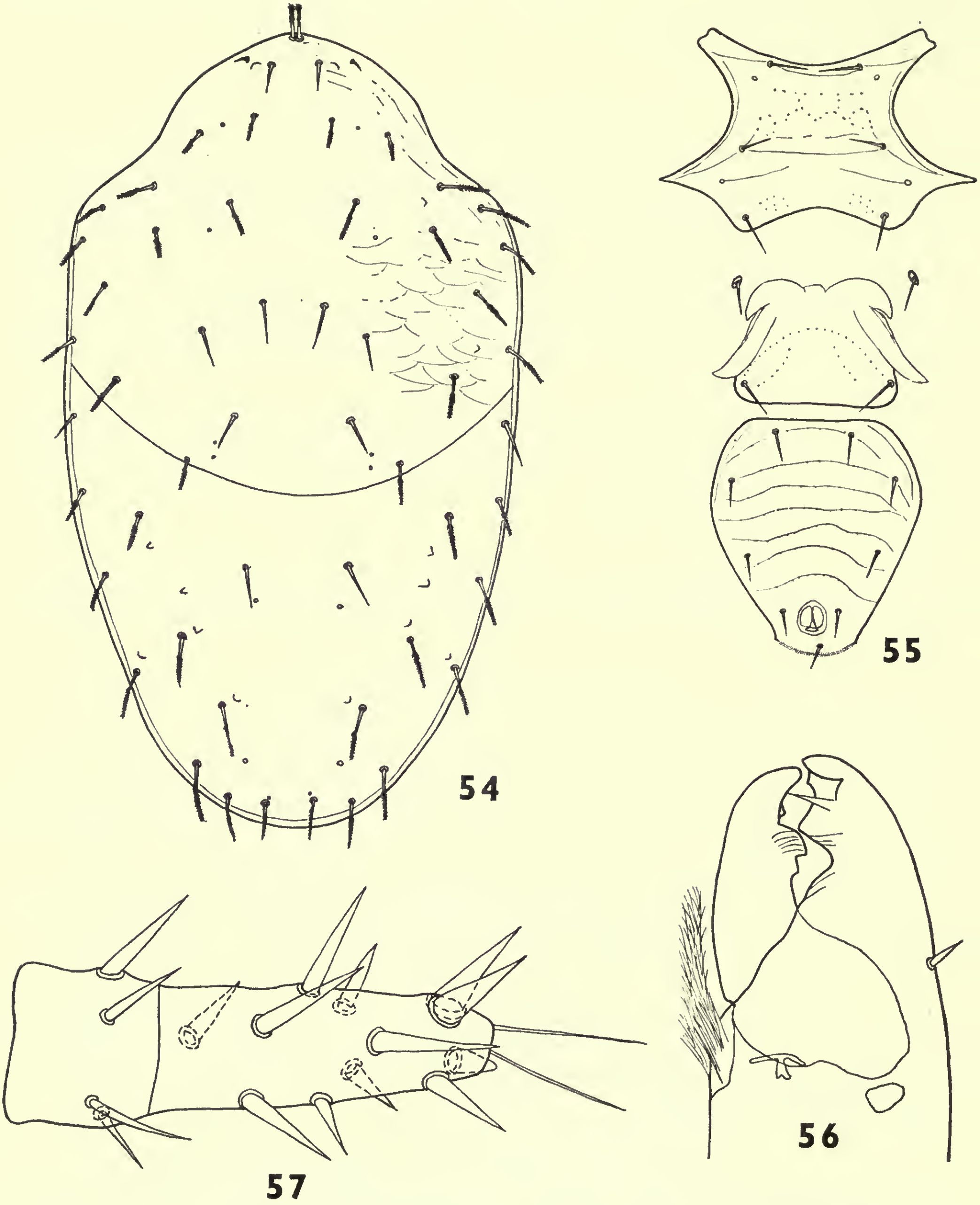
MALE. Unknown.

LOCALITIES. The holotype female (1961.7.14.545) on *Scarabaeus brahminus* Cast., collected by D. A. Thrower (1935–98) at Namakal, Salem, S. India; and one paratype (1961.7.14.546) on *Scarabaeus erichsoni* Harold, collected by J. J. Walker (1890–80) at Colombo, Ceylon.

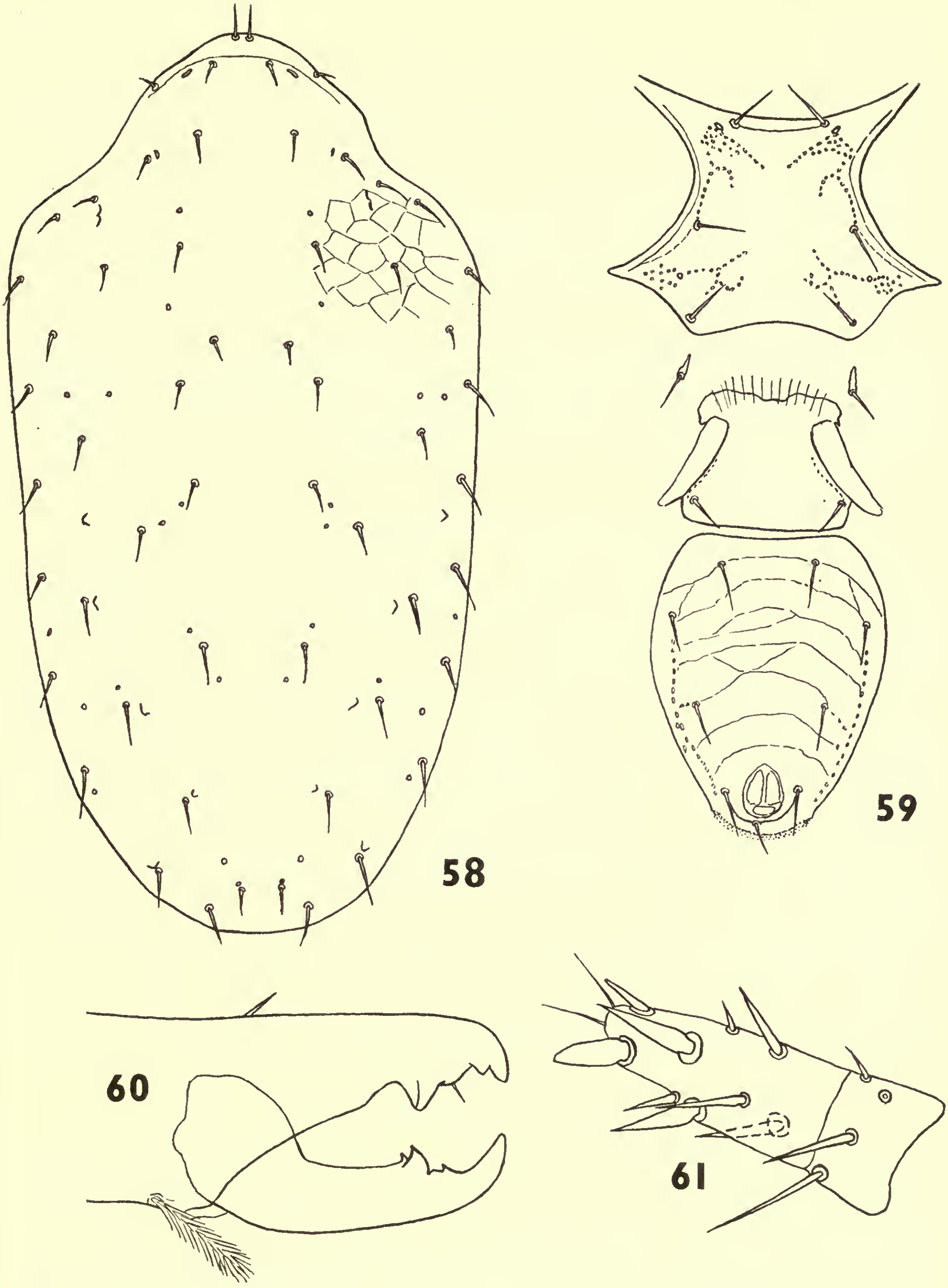
This species is named after Dr. G. W. Krantz.

Macrocheles longisetis sp. nov.

FEMALE. Dorsal shield (1,000μ long × 610μ wide) with faint scattered areas of reticulation only, and bearing 28 pairs of setae (Text-fig. 62). The majority of the setae are long (up to 132μ), slender and pilose distally, but the following six pairs



Figs. 54–57. *Macrocheles japonicus* sp. nov., female. Fig. 54, dorsal shield. Fig. 55, ventral shields. Fig. 56, chelicera. Fig. 57, tarsus II.



FIGS. 58–61. *Macrocheles krantzi* sp. nov., female. Fig. 58, dorsal shield. Fig. 59, ventral shields. Fig. 60, chelicera. Fig. 61, tarsus II.

are simple: i1, i4, i5, z2, z3 and J3. The verticals, i1, are two diameters of their bases apart.

Sternal shield granular, without *liniae*, markedly concave both anteriorly and posteriorly, sternal setae long (c. 110μ) (Text-fig. 63). Genital shield broad posteriorly, granular. Ventri-anal shield (370μ long × 320μ wide) finely granular and bearing nine simple setae.

The chelicera is shown in Text-fig. 64. The brush-like process of the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with six simple setae of which the erect *al* is the longest. Tarsus II (Text-fig. 65) 207μ, tibia II 129μ.

Male. Unknown.

Localities. The holotype female (1961.7.14.281) on *Mnematium marginatum* Péring, in the Fry collection (1905–100) from Kaffra, South Africa; and five paratypes also on *Mnematium marginatum* in South Africa, one (1961.7.14.282) collected by Pascoe (1893–60) in Little Namaqualand, and four (1961.7.14.283–286) in the Nevinson collection (1918–14) from Port Nolloth.

Macrocheles malabaricus sp. nov.

Female. Dorsal shield (651μ long × 415μ wide) finely granular, with only faint areas of reticulation, and bearing 28 pairs of setae (Text-fig. 66). In the unique specimen many of the setae are broken off at the tips, but they are probably all simple except the finely pilose pair J5.

The characteristic feature of this species is the ornamentation of the sternal shield which is granular with a unique linear pattern (Text-fig. 67). *L.m.t.* is undulating but does not reach the bases of setae II. *L.o.p.* curves up and meets *l.m.t.* towards the centre. The genital shield is granular and truncated posteriorly. The ventri-anal shield (206μ long × 164μ wide) is smooth in outline, finely granular and without any ornamentation. The nine setae are simple.

The chelicera is shown in Text-fig. 68. The brush of setae on the synarthrodial membrane is half the length of the movable digit. Six rows of deutosternal teeth. Tectum, Text-fig. 69.

Genu IV with seven stout simple setae. Tarsus II 152μ (Text-fig. 70), tibia II 101μ.

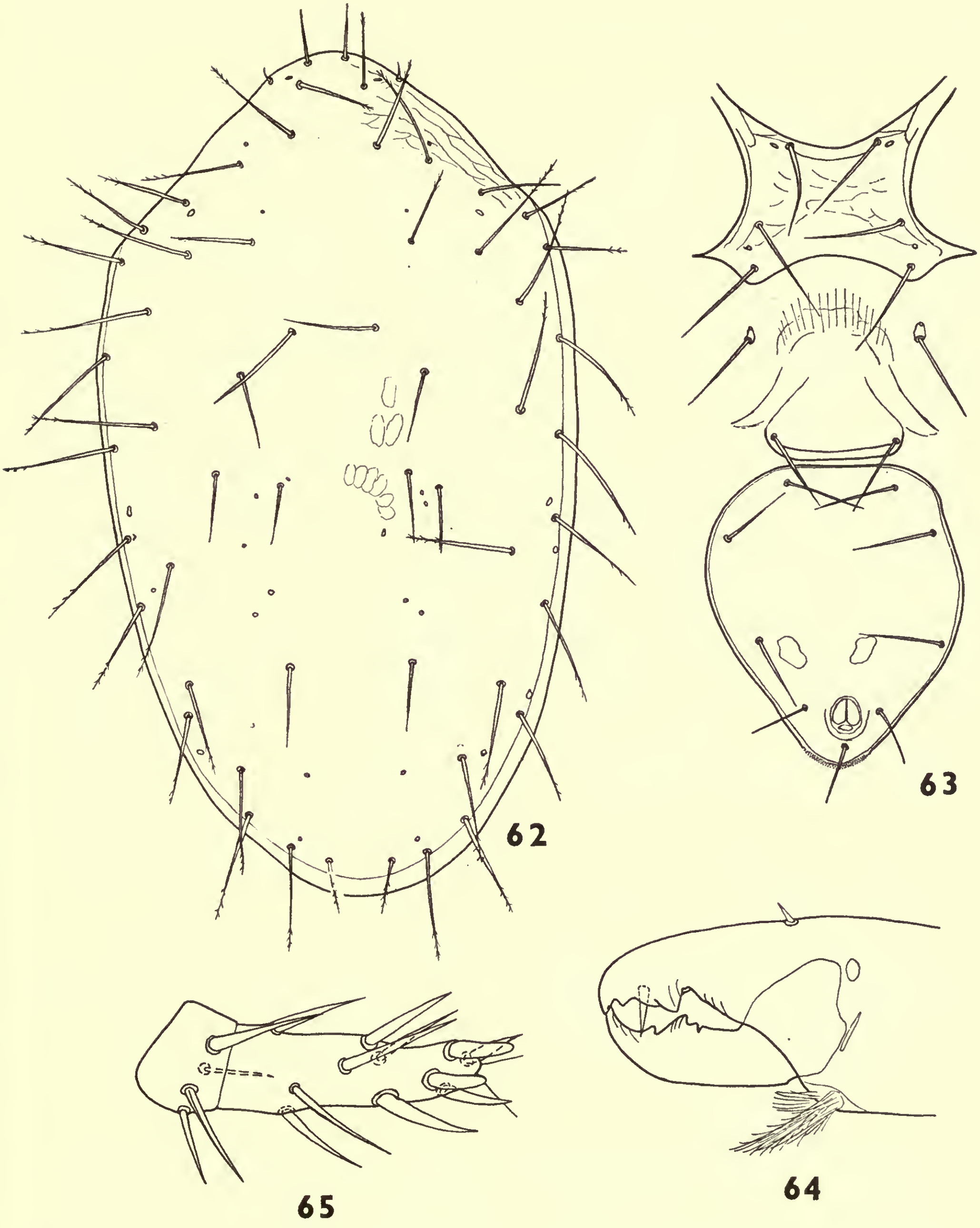
Male. Unknown.

Locality. A single female (1961.7.14.247) on *Gymnopleurus maculosus* McLeay in the Fry collection (1905–100) from Malabar, India.

Macrocheles marshalli sp. nov.

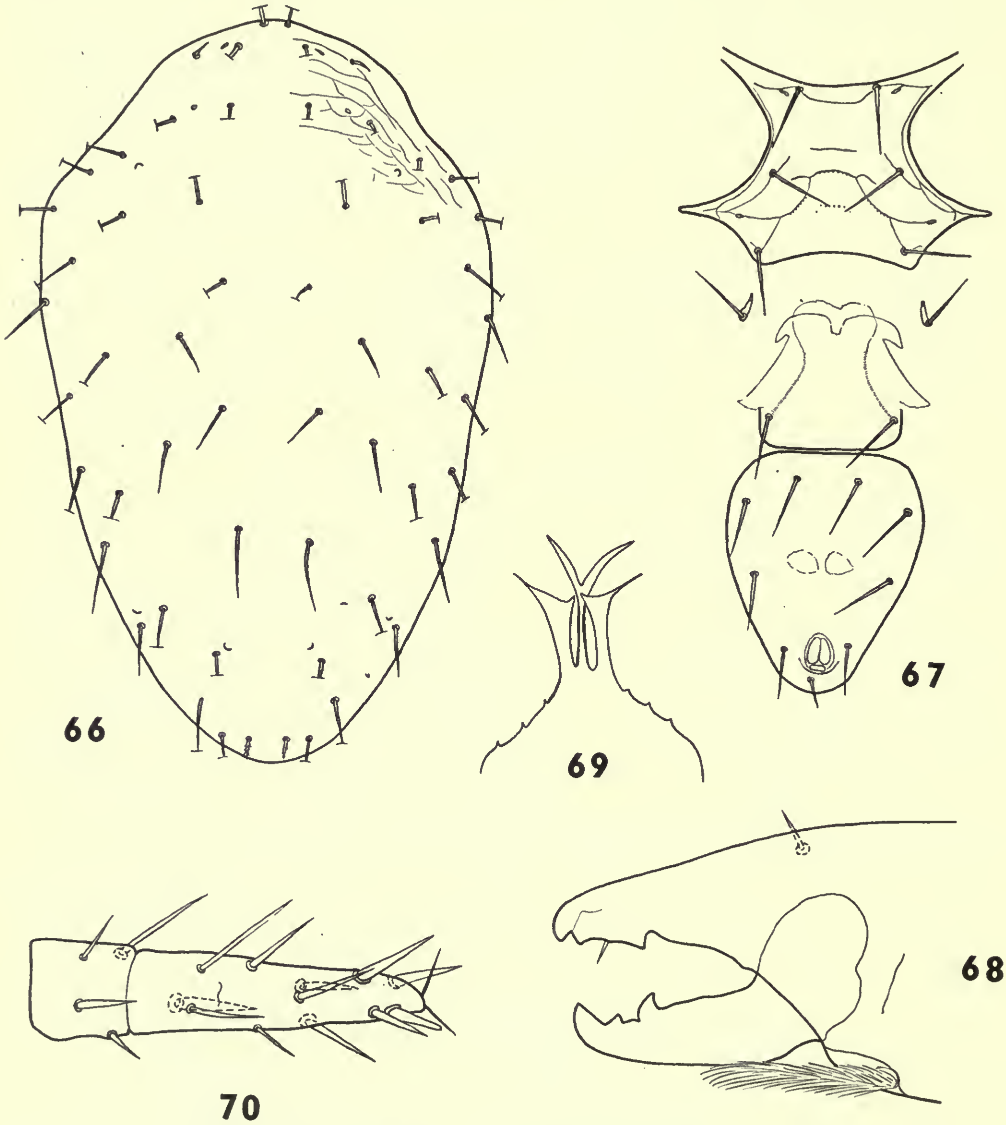
Female. Dorsal shield (826μ long × 467μ wide) finely granular, without reticulations, but with conspicuous pores and bearing 28 pairs of setae (Text-fig. 71). The majority of the dorsal setae are pilose distally with the exception of r1, i4, i5, z2, z3 and J3 which are simple. Setae J5 are short and palmate.

Sternal shield reticulated in its anterior half. *L.m.t.* slightly procurved, more pronounced medially, *l.o.p.* faint, extending towards *l.m.t.* (Text-fig. 72). Genital



FIGS. 62–65. *Macrocheles longisetis* sp. nov., female. Fig. 62, dorsal shield. Fig. 63, ventral shields. Fig. 64, chelicera. Fig. 65, tarsus II.

shield granular, without ornamentation, truncated posteriorly. Ventri-anal shield (289μ long × 258μ wide) granular and without ornamentation. A more attenuated form of ventri-anal shield is shown in Text-fig. 73.



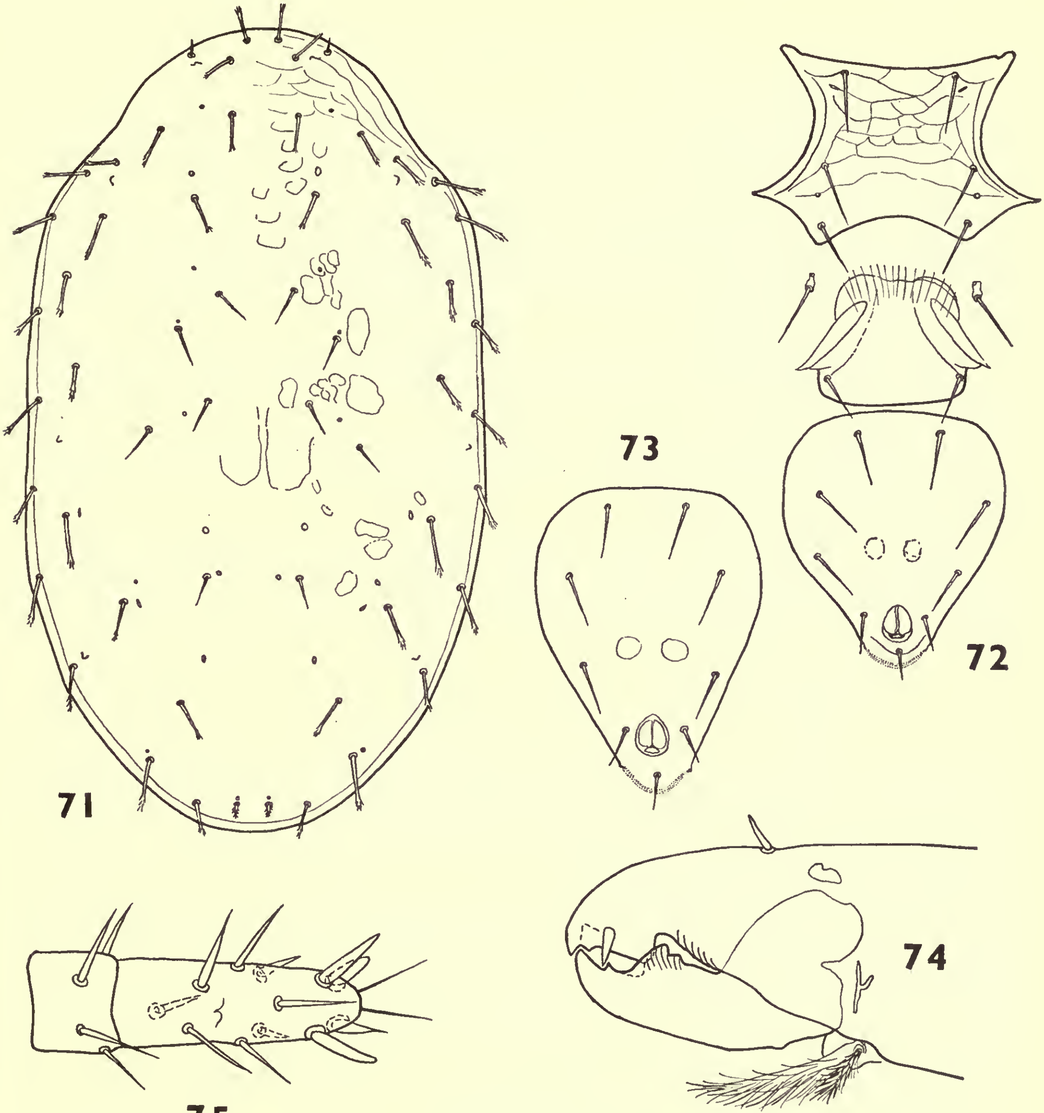
Figs. 66–70. *Macrocheles malabaricus* sp. nov., female. Fig. 66, dorsal shield. Fig. 67, ventral shields. Fig. 68, chelicera. Fig. 69, tectum. Fig. 70, tarsus II.

The chelicera is shown in Text-fig. 74. The brush of setae on the synarthrodial membrane is half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout setae of which pd_1 and pd_2 are finely pilose distally. Tarsus II (Text-fig. 75) 174μ, tibia II 103μ.

Male. Unknown.

Localities. The holotype female (1961.7.14.334) and one paratype (1961.7.14.335) from *Sceliages adamastor* Serv., collected by Sir Guy A. K. Marshall (1904–206) at the Umfuli River and Umtali, Mashonaland, Southern Rhodesia respectively; three paratypes (1961.7.14.336–338) also from *Sceliages adamastor*, collected by Sir Guy Marshall (1908–212) on the Upper Buzi River, Mozambique; two paratypes



Figs. 71–75. *Macrocheles marshalli* sp. nov., female. Fig. 71, dorsal shield. Fig. 72, ventral shields. Fig. 73, ventri-anal shield. Fig. 74, chelicera. Fig. 75, tarsus II.

(1961.7.14.340–341) again from *Sceliages adamastor*, collected by Pascoe (1893–60) at Delaqon, South Africa ; and one paratype (1961.7.14.339) on *Circellium bacchus* Fabr., collected by W. L. Distant (1911–383) at Brak Kloof Farm, Transvaal.

Macrocheles mexicanus sp. nov.

FEMALE. Dorsal shield (710μ long × 400μ wide) covered by faint punctate reticulations and bearing 28 pairs of setae (Text-fig. 76). The majority of the dorsal setae are simple, but setae i3, r4, z1, Z3, S4 and S5 are pilose distally.

Sternal shield large (180μ long) with a conspicuous unique pattern of areolations (Text-fig. 77). *L.ang.* short, other *liniae* absent. Genital shield broad, truncated posteriorly, and with punctate ornamentation. Ventri-anal shield (228μ long × 195μ wide) truncated anteriorly with conspicuous transverse punctate lines. The nine ventri-anal setae are simple.

The chelicera is shown in Text-fig. 78. The brush of setae on the synarthrodial membrane is a little over half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout setae all of which appear to be slightly pilose. Tarsus II (Text-fig. 79) 144μ, tibia II 88μ.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.262) and one paratype (1961.7.14.263) on *Phanaeus palliatus* Sturm., collected by the Biologia Centrali Americana expedition (1886–90) at Jalapa, Mexico.

Macrocheles natalensis sp. nov.

FEMALE. Dorsal shield (682μ long × 429μ wide) granular, with faint reticulations covering the entire shield, and with a procurved line medially. Twenty-eight pairs of setae (Text-fig. 80). The contiguous vertical setae, i1, are pilose distally and setae J5 are pilose along one margin.

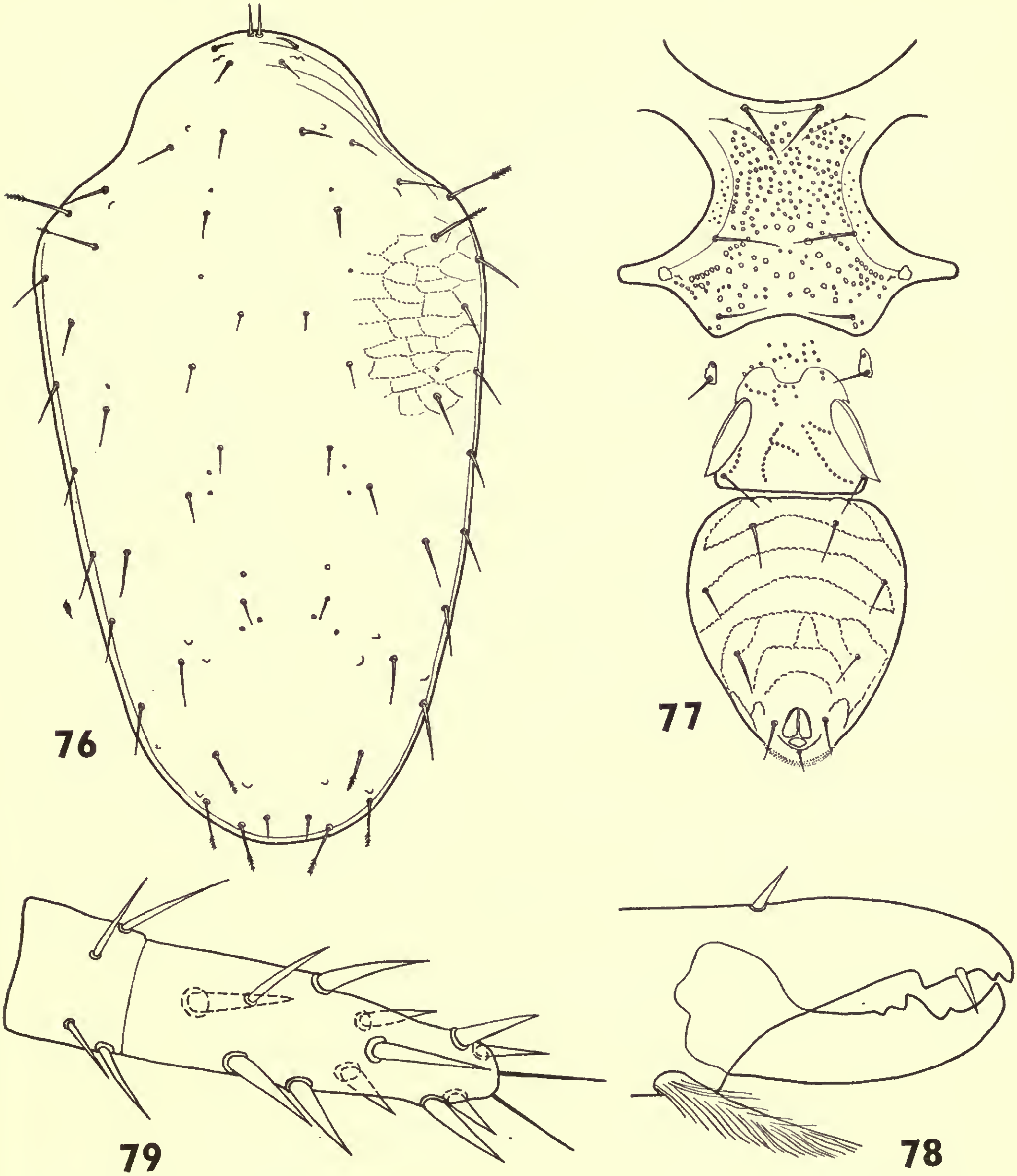
Sternal shield with a conspicuous pattern of areolations and *areae punctatae*. *L.m.t.* almost straight (Text-fig. 81). Genital shield broad, truncated posteriorly and with punctate ornamentation. Ventri-anal shield broader than long (220μ long × 240μ wide), truncated anteriorly and bearing nine simple setae. Ornamentation consisting of transverse punctate lines and strong granulation almost covering the entire surface.

The chelicera is shown in Text-fig. 82. Brush-like process of the synarthrodial membrane short. Six rows of deutosternal teeth.

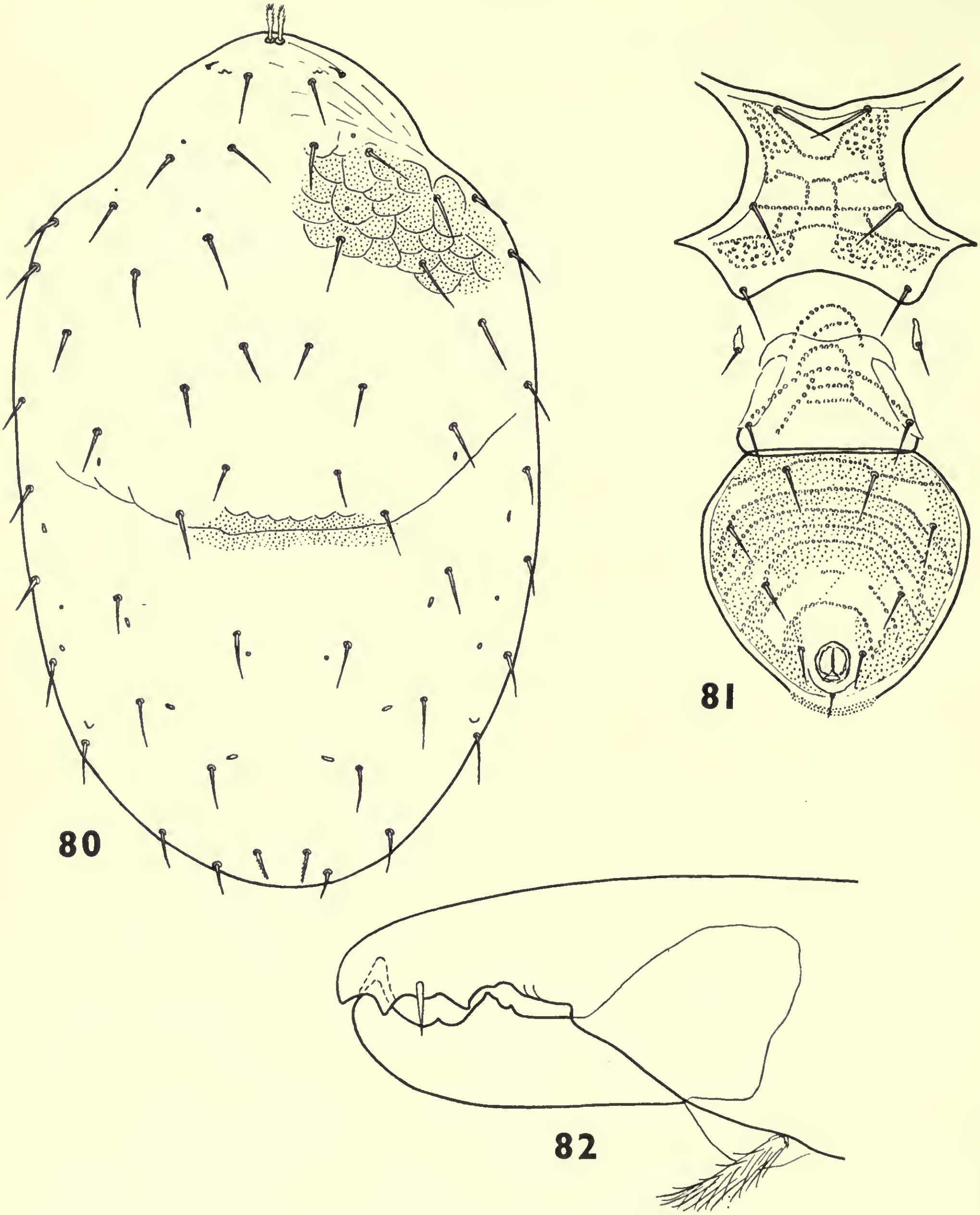
Genu IV with six stout setae of which pd_1, pd_2 and av are strongly palmate. The remaining three setae are simple. Chaetotaxy of legs mainly simple, though a number of the stouter setae are palmate. Tarsus II 110μ, tibia II 99μ.

MALE. Unknown.

LOCALITY. A single female (1961.7.14.552) on *Scarabaeus cuvieri* McLeay, collected by Sir Guy A. K. Marshall (1904–206) at Natal, South Africa.



FIGS. 76–79. *Macrocheles mexicanus* sp. nov., female. Fig. 76, dorsal shield. Fig. 77, ventral shields. Fig. 78, chelicera. Fig. 79, tarsus II.



Figs. 80–82. *Macrocheles natalensis* sp. nov., female. Fig. 80, dorsal shield. Fig. 81, ventral shields. Fig. 82, chelicera.

Macrocheles nevernalis sp. nov.

FEMALE. Dorsal shield (649–737μ long × 385–434μ wide) finely granular and faintly reticulated, and bearing 28 pairs of setae (Text-fig. 83). With a few exceptions, all setae are simple. The verticals, i1, are pilose distally and have their bases well separated, and S2–S5, Z2, Z3 and J5 are pilose distally. Setae J2 absent.

Sternal shield granular (Text-fig. 84). *L.m.t.* almost straight, *l.o.p.* short. Genital shield broad and granular. Ventri-anal shield pear-shaped (220–247μ long × 181–209μ wide), finely granular and with recurved transverse lines. The nine setae are simple.

The chelicera is shown in Text-fig. 85. The brush-like process of the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with six setae of which two or more are slightly divided distally. Tarsus II (Text-fig. 86) 140μ, tibia II 90μ, all setae simple.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.547) and four paratypes (1961.7.14.548–551) on *Scarabaeus brahminus* Cast., collected by D. A. Thrower (1935–98) at Namakal, Salem, S. India.

Macrocheles nevinsoni sp. nov.

FEMALE. Dorsal shield (760μ long × 475μ wide) with only a few faint traces of ornamentation mainly around the margins, and bearing 28 pairs of strongly-bipectinate setae (Text-fig. 87). Setae r1, z2, i5, J3 and J5 are the shortest (c. 54μ) whilst the remaining setae are much longer (up to 143μ) (Text-fig. 88).

Sternal shield narrow, with punctate ornamentation. *L.m.t.* very slightly procurved, *l.arc.* recurved (Text-fig. 89). Genital shield truncated posteriorly and with punctate lines. Ventri-anal shield (260μ long × 205μ wide) with conspicuous punctate transverse lines and nine simple setae.

The chelicera is shown in Text-fig. 90. The brush of setae on the synarthrodial membrane is about a third the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout strongly-bipectinate setae. Tarsus II 155μ (Text-fig. 91), tibia II 110μ. A number of the stout setae on legs II–IV are also bipectinate.

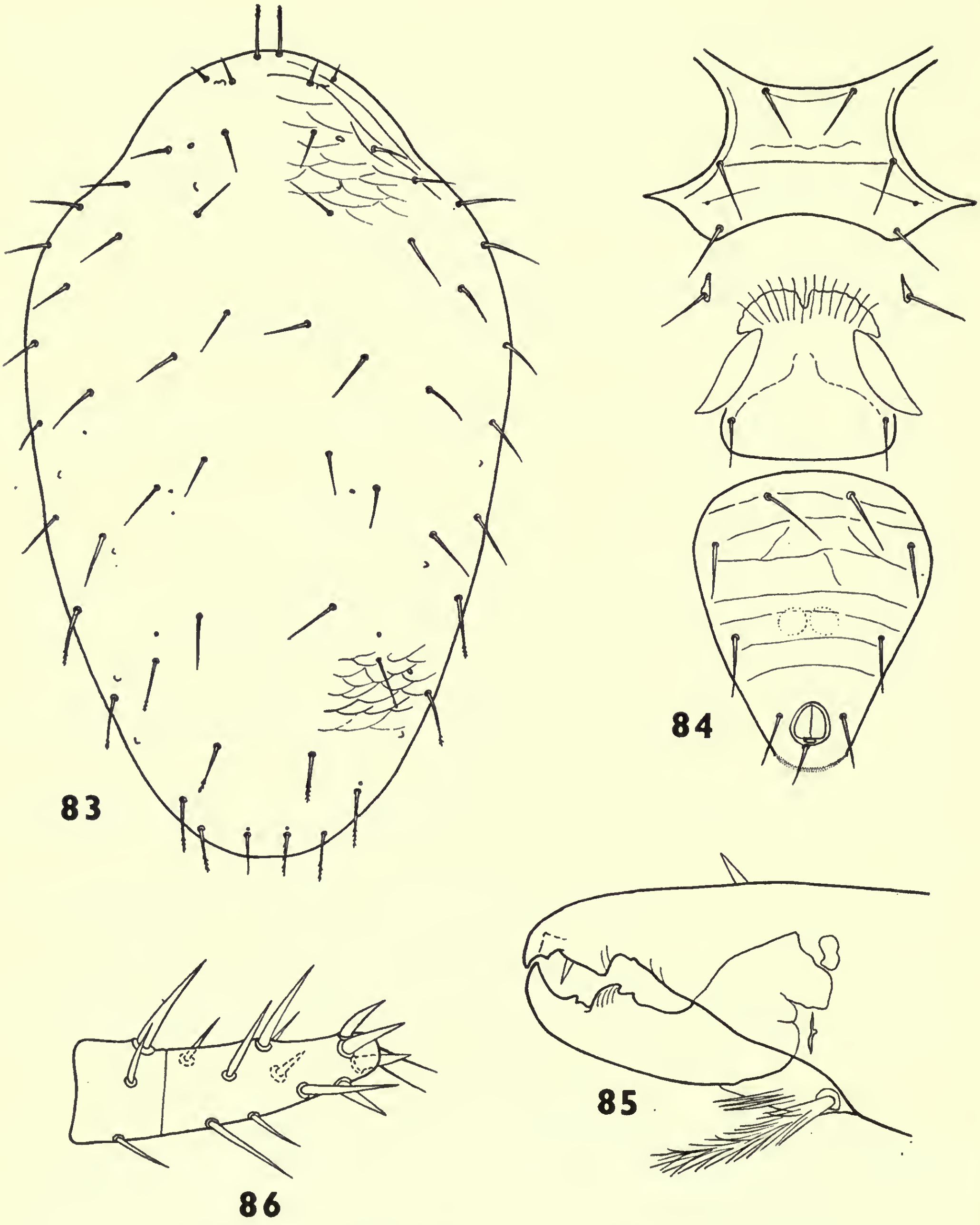
MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.231) and four paratypes (1961.7.14.232–235) on *Megathopa argentina* Gillet, in the Nevinson collection (1918–14) from Rio Salado, Argentina.

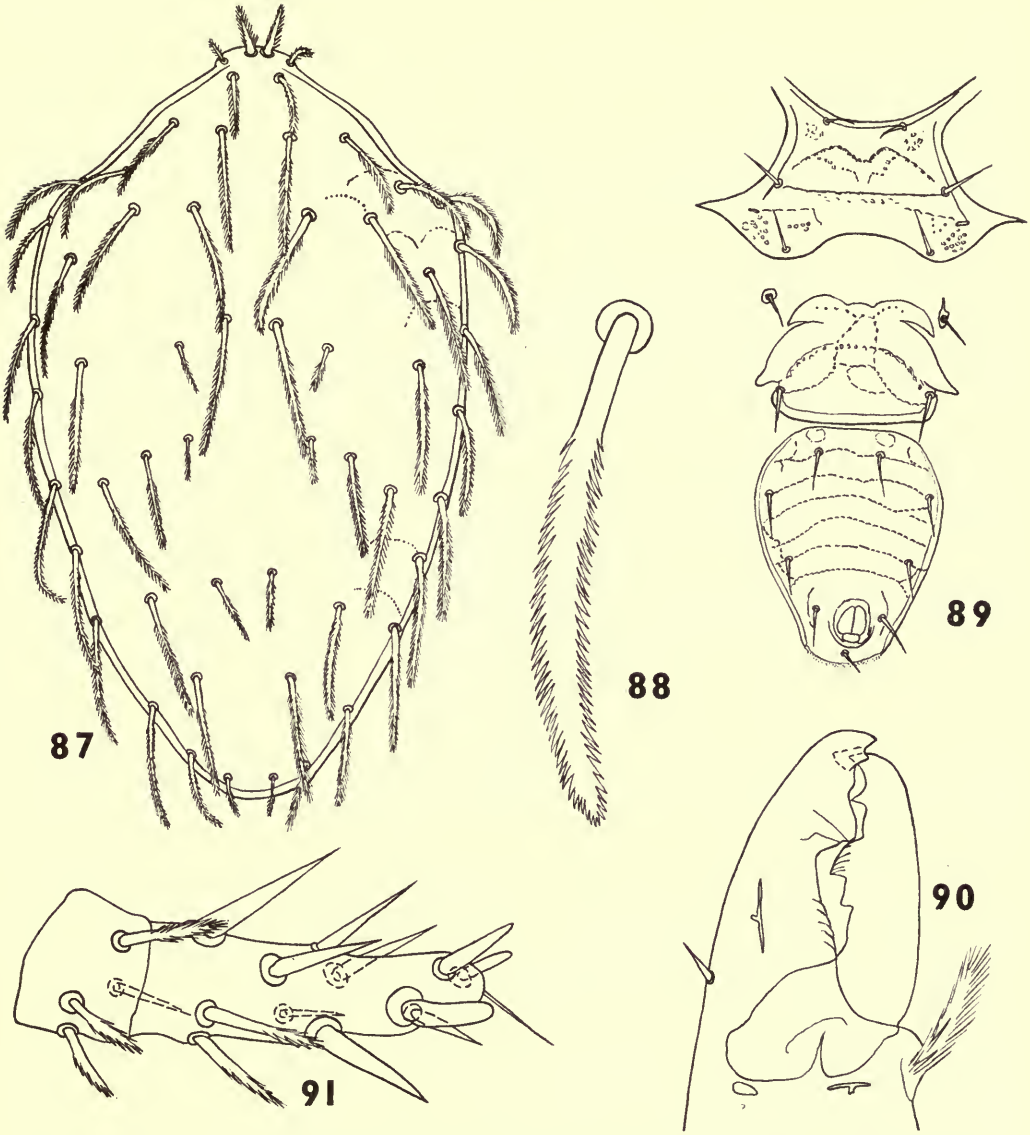
Macrocheles pisentii (Berlese, 1882)

Gamasus tardus var. *Pisentii* Berlese, A., 1882, *Bull. Soc. ent. Ital.* **14** : 112, figs.
Holostaspis pisentii, Berlese, A., 1887, *Acari, Myriopoda et Scorpiones, etc., Fasc.* 76, No. 1.
Macrocheles pisentii Evans, G. O. and Browning, E., 1956, *Bull Brit. Mus.* (*nat. Hist.*), *Zool.* **4** : 13, figs.

FEMALE. Dorsal shield (790–830μ long × 450–600μ wide) finely granular with faint reticulation around the margins, and bearing 28 pairs of setae. The dorsal shield is figured by Evans & Browning (1956). Setae J5 are short and palmate



Figs. 83–86. *Macrocheles nevernalis* sp. nov., female. Fig. 83, dorsal shield. Fig. 84, ventral shields. Fig. 85, chelicera. Fig. 86, tarsus II.



Figs. 87–91. *Macrocheles nevinsoni* sp. nov., female. Fig. 87, dorsal shield. Fig. 88, dorsal seta. Fig. 89, ventral shields. Fig. 90, chelicera. Fig. 91, tarsus II.

(Text-fig. 92); the remaining setae are all simple. The vertical setae, i1, are two diameters apart.

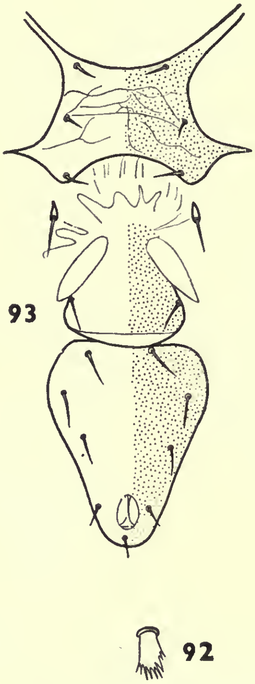
Sternal shield concave posteriorly, granular, with faint reticulations on some specimens. *L.m.t.* slightly recurved (Text-fig. 93). Genital shield granular, without ornamentation. Ventri-anal shield (260μ long × 190μ wide) granular, attenuated posteriorly and bearing nine simple setae.

The chelicerae and tectum, which are typical of the genus, are figured by Evans & Browning (*loc. cit.*). Five rows of deutosternal teeth.

Genu IV with six stout simple setae. Chaetotaxy of legs simple.

MALE. Unknown.

DISTRIBUTION. This species was collected originally from *Scarabaeus semipunctatus* F. in Italy and has subsequently been obtained from a number of localities in Great Britain. The present collection contains many females on *Scarabaeus semipunctatus* from Savoy & Perpignan in France, from Majorca, Algeria and the Sahara; on *Scarabaeus sacer* L. from Egypt and the Persian Gulf; on *Scarabaeus puncticollis* Latr. from Tunisia and N. Sinai; and from *Scarabaeus socotranus* Gillet from Socotra.



FIGS. 92–93. *Macrocheles pisentii* (Berlese), female. Fig. 92, dorsal seta J5. Fig. 93, ventral shields.

Macrocheles plumosus sp. nov.

FEMALE. Dorsal shield (711μ long × 415μ wide) with a very characteristic areolate pattern, and bearing 28 pairs of setae (Text-fig. 94). The verticals, i1, are extremely short and palmate, r1 are short and pilose, and J5 are finely bipectinate. The remaining 25 pairs are up to 107μ long and very markedly bipectinate. J2 absent.

Sternal shield covered entirely by a conspicuous reticulation. *L.m.t.* entire, slightly undulating, other structural lines forming an integral part of the ornamentation (Text-fig. 95). Genital shield broad, truncated posteriorly, and with some ornamentation. Ventri-anal shield (247μ long × 247μ wide) pear-shaped, with conspicuous transverse lines and lateral ornamentation. The post-anal seta is short and pilose, the remaining eight are simple.

The chelicera is shown in Text-fig. 96. The brush of setae on the synarthrodial membrane is short. Five rows of deutosternal teeth.

Genu IV with six strongly pilose setae. Tarsus II 135μ (Text-fig. 97), tibia II 88μ.

MALE. Dorsal shield (507μ long × 361μ wide) with ornamentation and chaetotaxy as in the female, except that z2 and i5 are simple. Sterniti-genital shield with five pairs of simple setae ; ornamentation as in the female sternal shield. Ventri-anal shield (169μ long × 169μ wide) with ornamentation and chaetotaxy similar to the female.

The chelicera is shown in Text-fig. 98. The spermatophoral process is slender. Synarthrodial brush very short.

Genu IV with six pilose setae. Femur II with a thumb-like spur ventrally. Remaining chaetotaxy of the legs typical.

LOCALITY. The holotype female (1952.9.8.478), allotype male (1952.9.8.481) and two paratype females (1952.9.8.479–480) on " Beetle F240 " collected by the Oxford University Expedition to Sarawak, 28.x.1932.

Macrocheles pyriformis sp. nov.

FEMALE. Dorsal shield (795μ long × 415μ wide) granular and with faint reticulations, more noticeably anteriorly, and bearing 28 pairs of setae (Text-fig. 99). All setae are simple except J5 which are short and palmate. The verticals, i1, are well separated.

Sternal shield squarish, with a linear ornamentation, *liniae* obscured (Text-fig. 100). Genital shield granular, without ornamentation, truncated posteriorly. Ventri-anal shield (268μ long × 227μ wide) markedly attenuated posteriorly, finely granular and with faint transverse lines. The nine ventri-anal setae are simple.

The chelicera is shown in Text-fig. 101. The brush-like process of the synarthrodial membrane is about half the length of the movable digit. Seven rows of deutosternal teeth.

Genu IV with six stout setae all of which are longer than usual and simple. Tarsus II (Text-fig. 102) 126μ, tibia II 101μ.

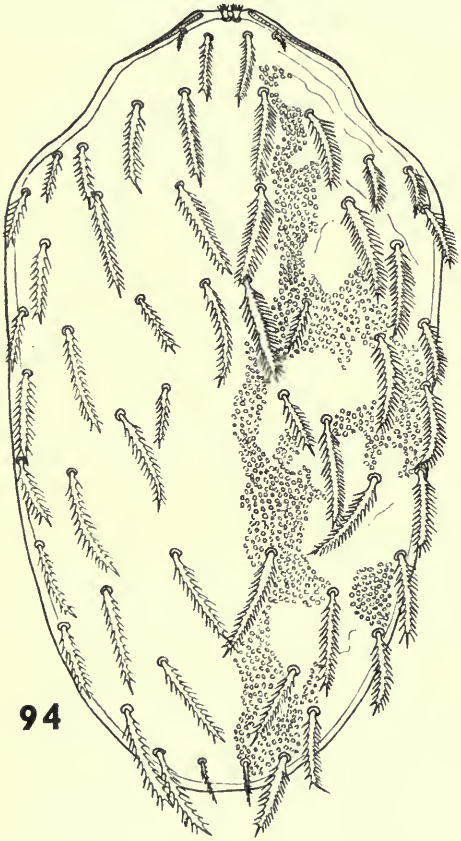
MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.287) and six paratypes (1961.7.14.288–293) on *Mnematium ritchiei* McLeay in the Nevinson collection (1918–14) labelled " Tripolitania 1899 ".

Macrocheles rhodesi sp. nov.

FEMALE. Dorsal shield (726μ long × 473μ wide) with very faint reticulations, a faint procurved transverse line mid-dorsally, and bearing 28 pairs of setae (Text-fig. 103). The vertical setae, i1, with their bases touching, are directed anteriorly and are slightly pilose distally. Setae J5 are lightly bipectinate along their entire lengths; all remaining setae are simple.

Sternal shield granular, faint traces of punctate ornamentation, *l.m.t.* almost straight, other *liniae* absent (Text-fig. 104). Genital shield broad, truncated pos-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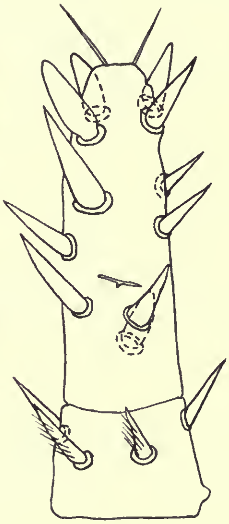
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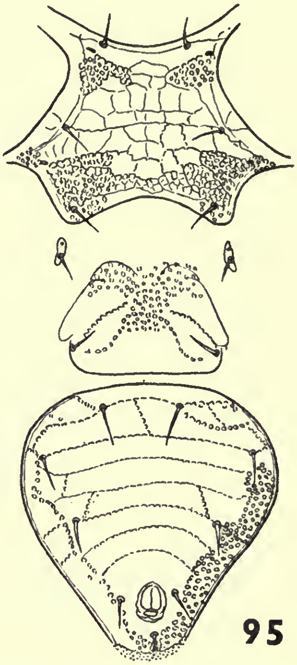
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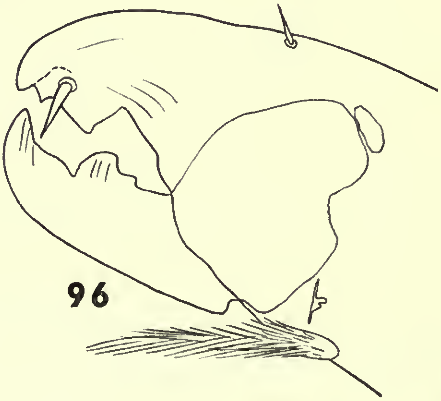
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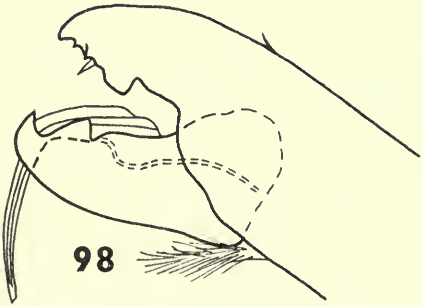
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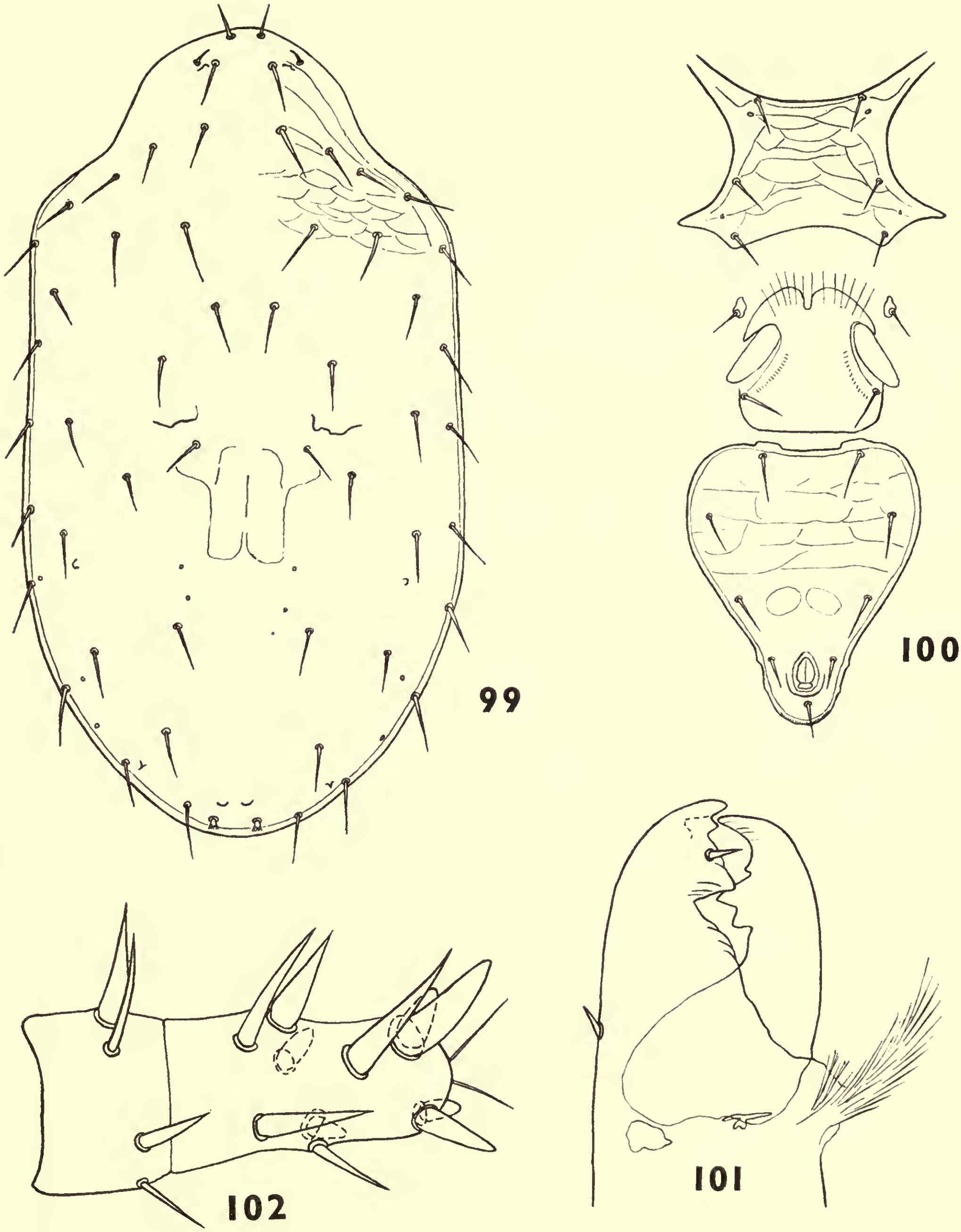
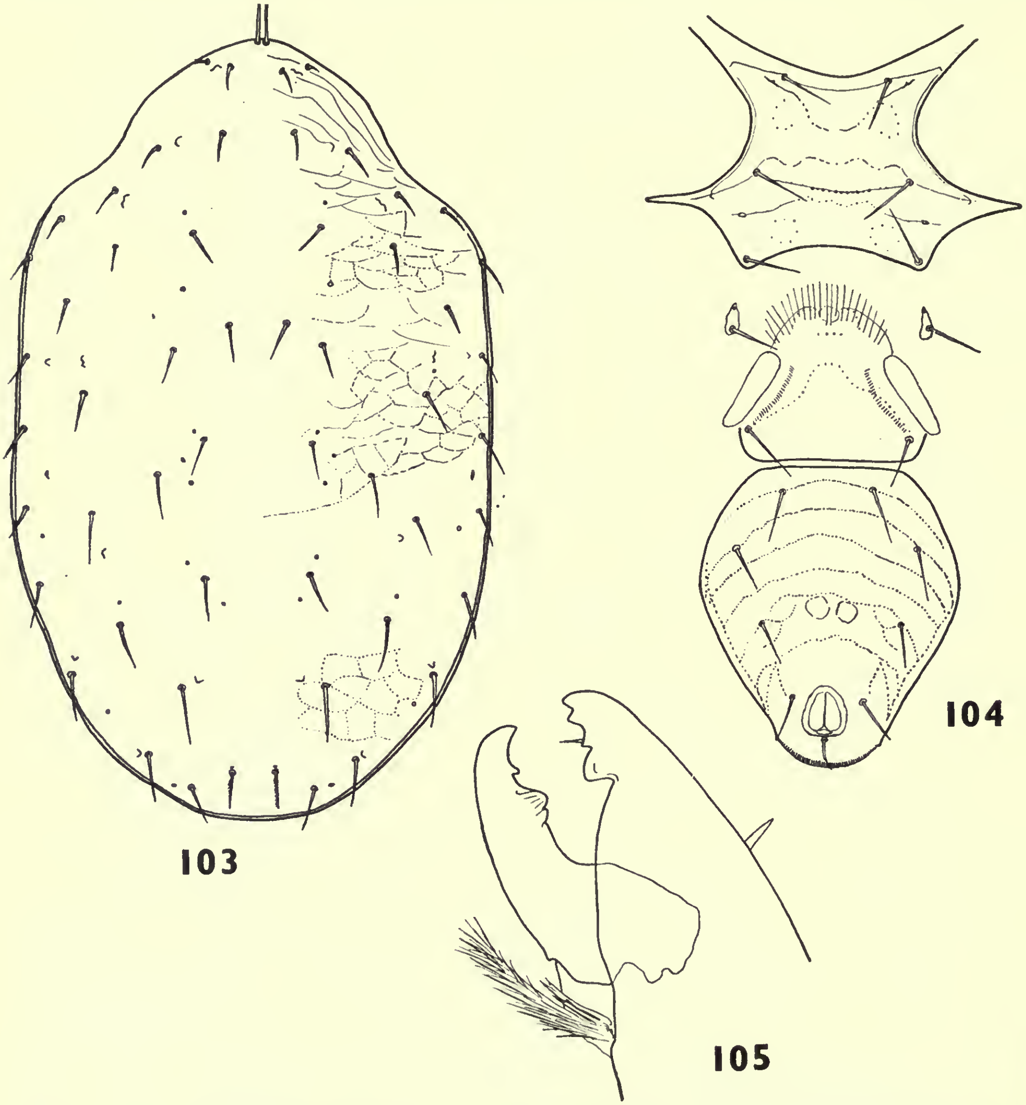
FIGS. 94–98. *Macrocheles plumosus* sp. nov. Fig. 94, dorsal shield of female. Fig. 95, ventral shields of female. Fig. 96, chelicera of female. Fig. 97, tarsus II of female. Fig. 98, chelicera of male.



FIGS. 99–102. *Macrocheles pyriformis* sp. nov., female. Fig. 99, dorsal shield. Fig. 100, ventral shields. Fig. 101, chelicera. Fig. 102, tarsus II.

teriorly. Ventri-anal shield (240μ long × 220μ wide) ovoid, truncated anteriorly, with strongly recurved transverse lines and bearing nine simple setae.

The chelicera is shown in Text-fig. 105. The brush-like process of the synarthrodial membrane is half the length of the movable digit. Six rows of deutosternal teeth.



FIGS. 103–105. *Macrocheles rhodesi* sp. nov., female. Fig. 103, dorsal shield. Fig. 104, ventral shields. Fig. 105, chelicera.

Genu IV with six stout setae of which *av* and *al* only are simple, the four dorsal setae being slightly pilose distally. Tarsus II 143μ, tibia II 95μ.

MALE. Unknown.

LOCALITIES. The holotype female (1961.7.14.342) and five paratypes (1961.7.14.343–347) on *Gymnopleurus azureus* Fabr., collected in the Serenje District, NE. Rhodesia, by S. A. Neave (1907–230); four paratypes (1961.7.14.348–351) on *Sebasteos laticeps* Péring in the Nevinson collection (1918–14) from Adelaide, Cape Province; and a single paratype (1961.7.14.352) on *Sebasteos galenus* Westw., collected by Sir Guy A. K. Marshall (1931–138) at Salisbury, Southern Rhodesia.

Macrocheles rykei sp. nov.

FEMALE. Dorsal shield (792–902μ long × 484–524μ wide) granular with a finely dotted reticulated pattern, and bearing 28 pairs of setae (Text-fig. 106). The following setae are pilose distally: i2, s2, s5, s6, r4, r5, r7, Z1, S4, S5 and J5; the remainder are simple. The verticals, i1, are well separated and directed anteriorly.

Sternal shield granular, irregularly concave posteriorly. *L.m.t.* slightly procurved, undulating, other *liniae* scarcely visible (Text-fig. 107). Genital shield finely granular, truncated posteriorly. Ventri-anal shield (242–286μ long × 187–242μ wide) slightly attenuated posteriorly, finely granular and with transverse dotted lines. The nine setae are simple.

The chelicera is shown in Text-fig. 108. The brush-like process of the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with six stout setae. Tarsus II 177μ (Text-fig. 109), tibia II 113μ.

MALE. Unknown.

LOCALITIES. The holotype female (1961.7.14.391) and one paratype (1961.7.14.392) on *Scarabaeus bonellii* McLeay, collected by W. L. Distant (1911–383) at Cape Town; eight paratypes (1961.7.14.393–400) also on *Scarabaeus bonellii*, collected by Miss A. Mackie (1948–525) at Nieuwoudtville; and nine paratypes (1961.7.14.401–409) on *Gymnopleurus unicolor* Fåhr., collected by R. E. Turner (1924–109) at Port St. John, Pondoland. All localities are in South Africa.

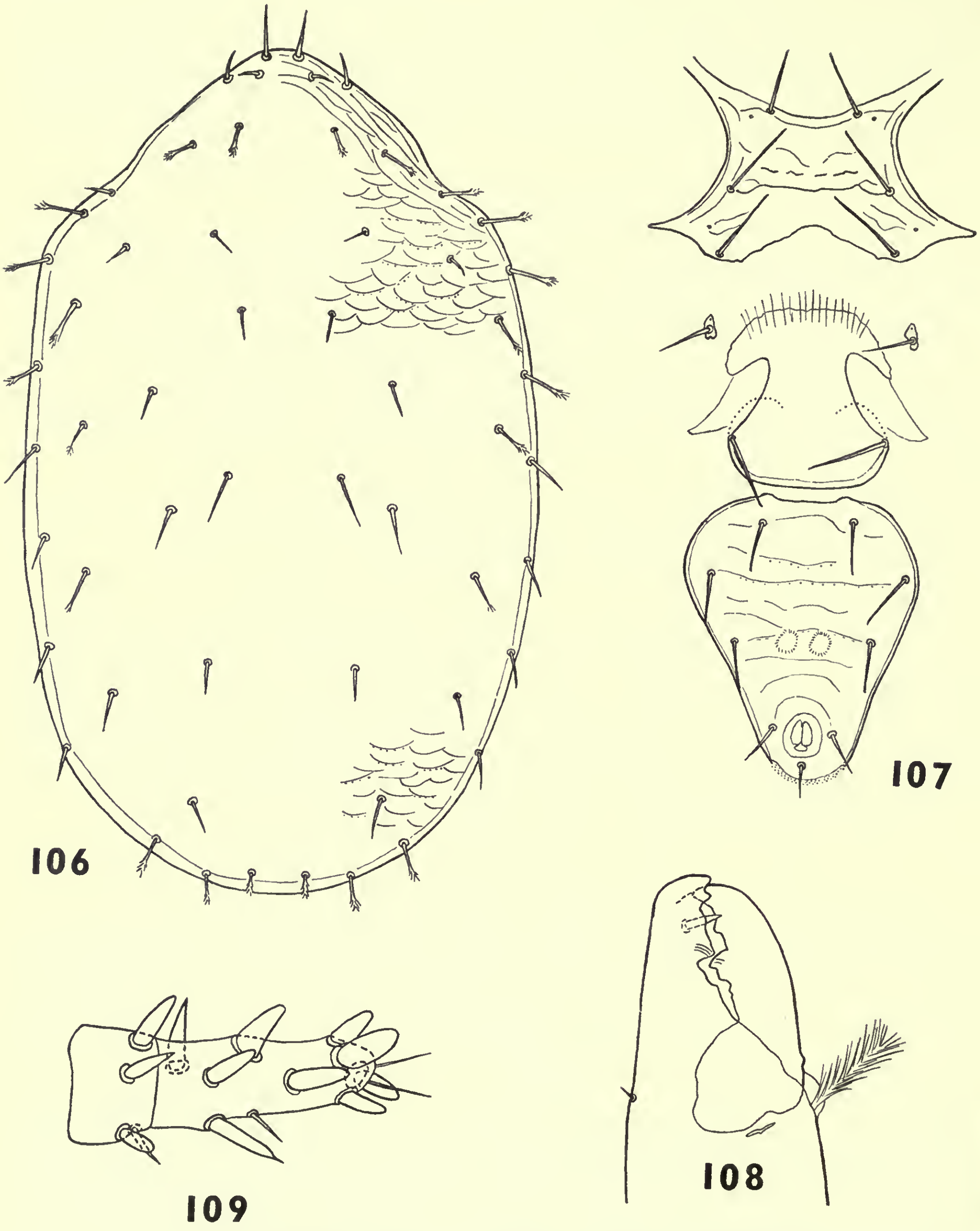
This species is named after Dr. P. A. J. Ryke.

Macrocheles sternalis sp. nov.

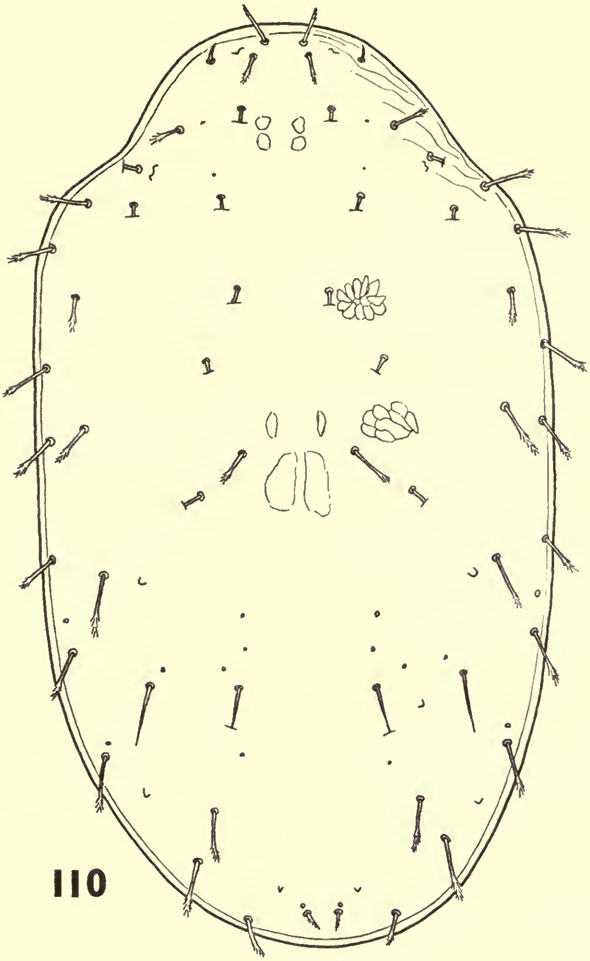
FEMALE. Dorsal shield (910μ long × 518μ wide) finely granular, with only traces of ornamentation, and bearing 28 pairs of setae (Text-fig. 110). The chaetotaxy of the dorsal shield is not complete in the unique specimen, but, nevertheless, the verticals, i1, are separated by about three times the diameter of their bases, and it would appear that all the setae are pilose distally with the exception of r1 which are short and spinose.

Sternal shield granular, *liniae* very indistinct, but with a U-shaped mark medially (Text-fig. 111). In the unique specimen the right metasternal shield is fused with the sternal shield. Genital shield broad, shallow, and granular. Ventri-anal shield (320μ long × 330μ wide) with an irregular concavity anteriorly, finely granular but without distinct ornamentation. With the exception of the paranals, which are simple, the remaining seven ventri-anal setae are slightly split distally.

The chelicera is shown in Text-fig. 112. The brush-like process of the synarthrodial membrane is half the length of the movable digit. Six rows of deutosternal teeth.



FIGS. 106–109. *Macrocheles rykei* sp. nov., female. Fig. 106, dorsal shield. Fig. 107, ventral shields. Fig. 108, chelicera. Fig. 109, tarsus II.



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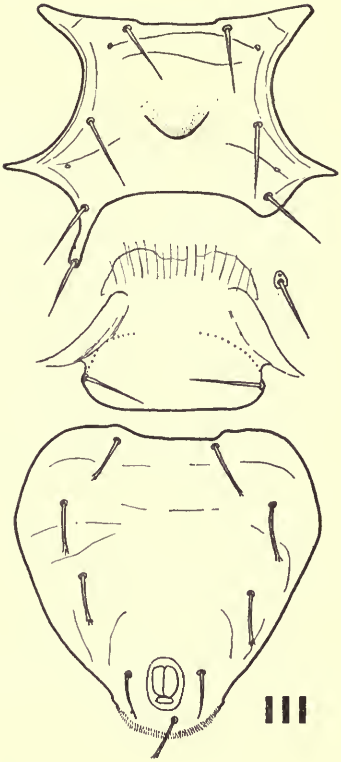

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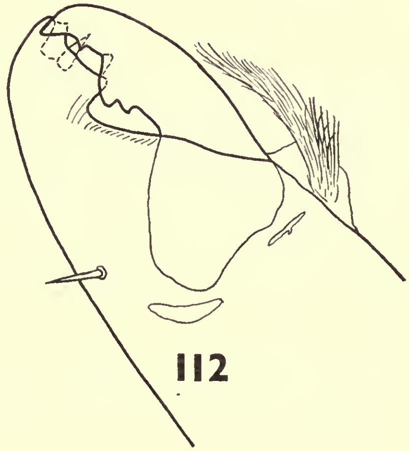

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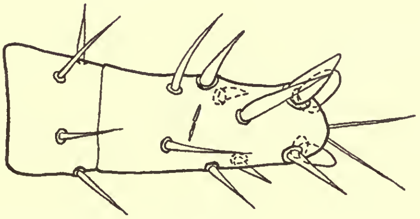

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FIGS. 110–113. *Macrocheles sternalis* sp. nov., female. Fig. 110, dorsal shield. Fig. 111, ventral shields. Fig. 112, chelicera. Fig. 113, tarsus II.

Genu IV with six setae, all of which are pilose distally. Tarsus II (Text-fig. 113) 162μ, tibia II 114μ.

Male. Unknown.

Locality. A single female (1961.7.14.333) on *Sceliages augias* Gillet, collected by Dr. L. Lloyd (1913–170) in Northern Rhodesia.

Macrocheles telamoni sp. nov.

Female. Dorsal shield (826μ long × 467μ wide) with areas of punctate ornamentation, and bearing 28 pairs of setae. There are a pair of rounded protuberances at the bases of setae Z1 (Text-fig. 114). With the exception of setae i5, which are simple, all setae are strongly bipectinate.

Sternal shield finely granular, with a coarse area of punctations exterior to the posterior sternal setae (Text-fig. 115). *L.m.t.* slightly recurved, discontinuous medially, *l.arc.* only rudimentary. Genital shield granular, truncated posteriorly. Ventri-anal shield (240μ long × 197μ wide) truncated anteriorly, granular, and with transverse lines, all setae simple.

The chelicera is shown in Text-fig. 116. The brush-like process of the synarthrodial membrane is about two-thirds the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with seven stout setae, all of which are bipectinate. Tarsus II (Text-fig. 117) 177μ, tibia II 113μ.

Male. Unknown.

Locality. The holotype female (1961.7.14.353) and four paratypes (1961.7.14.354–357) on *Phanaeus telamon* Erichs., collected by the Biologia Centrali Americana expedition (1886–90) at Volcan de Chiriqui, Panama.

Macrocheles thomasseti sp. nov.

Female. Dorsal shield (711μ long × 435μ wide) finely granular and with areas of reticulation, and bearing 28 pairs of setae (Text-fig. 118). Setae r4 and r5 are lightly pilose distally and J5 are short and bipectinate. The remaining setae are simple although a few may appear split distally.

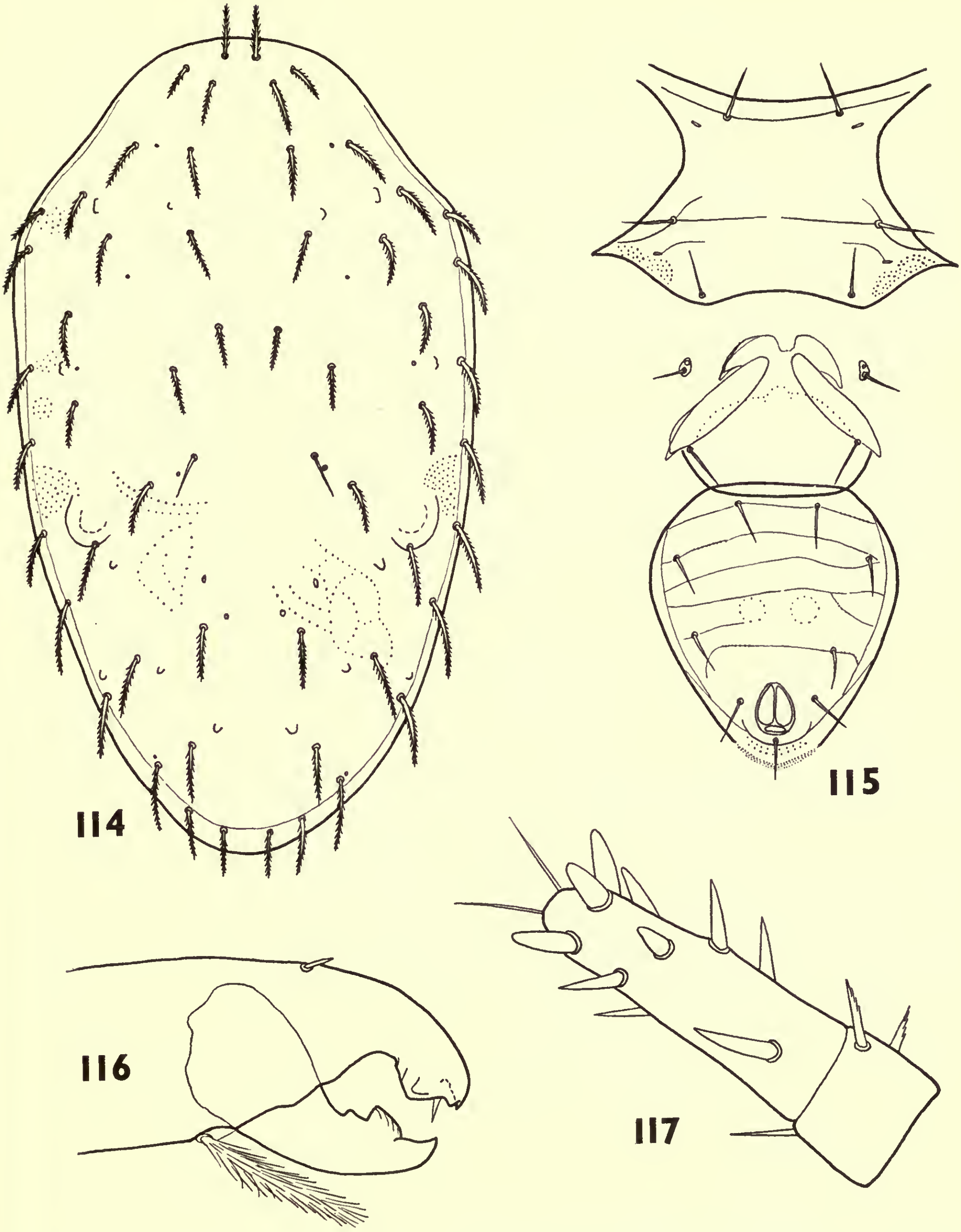
Sternal shield granular. *L.m.t.* absent, *l.arc.* widely recurved, *l.o.p.* short (Text-fig. 119). Genital shield granular, truncated posteriorly. Ventri-anal shield (237μ long × 185μ wide) granular, devoid of any ornamentation and bearing nine simple setae.

The chelicera is shown in Text-fig. 120. The brush-like process of the synarthrodial membrane is half the length of the movable digit. Six rows of deutosternal teeth.

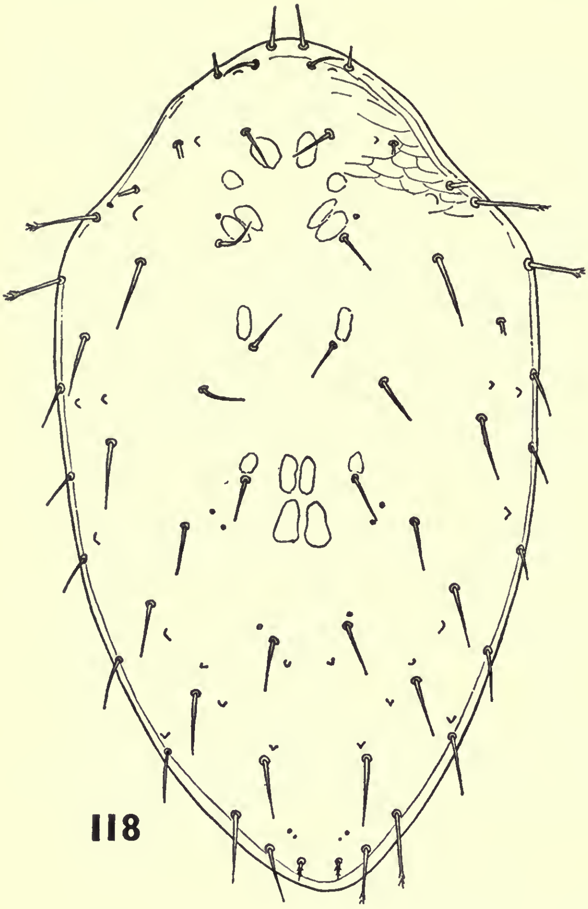
Genu IV with six stout setae all of which are slightly pectinate at their tips. Tarsus II (Text-fig. 121) 128μ, tibia II 93μ.

Male. Unknown.

Locality. A single female (1961.7.14.375) on *Scarabaeus gangeticus* Cast., collected by H. P. Thomasset (1900–122) at Sterkfontein, Transvaal.



FIGS. 114–117. *Macrocheles telamoni* sp. nov., female. Fig. 114, dorsal shield. Fig. 115, ventral shields. Fig. 116, chelicera. Fig. 117, tarsus II.



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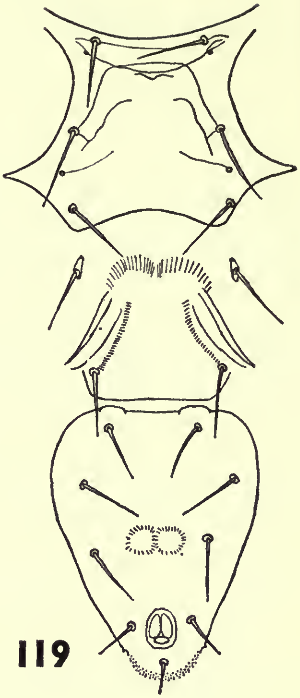

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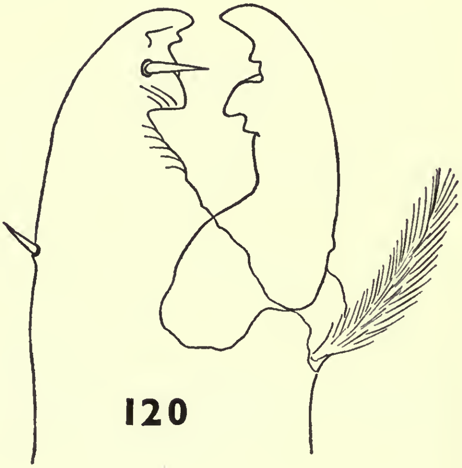

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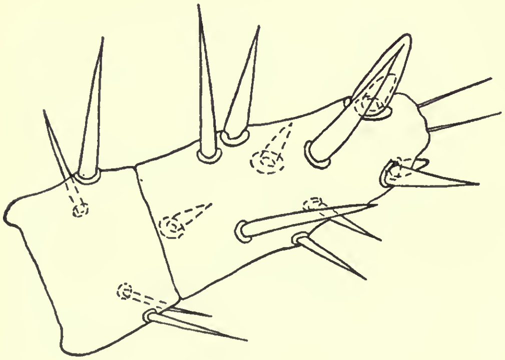


121

FIGS. 118–121. *Macrocheles thomasseti* sp. nov., female. Fig. 118, dorsal shield. Fig. 119, ventral shields. Fig. 120, chelicera. Fig. 121, tarsus II.

Macrocheles transversus sp. nov.

FEMALE. Dorsal shield (670μ long × 425μ wide) with conspicuous transverse reticulations and bearing 28 pairs of setae (Text-fig. 122). The majority of the dorsal setae are simple but certain ones in the r- and S-series may be finely pectinate distally. Setae i1 are about one and a half diameters apart; J5 are short and pectinate.

Sternal shield broad and with conspicuous ornamentation. *L.m.t.* slightly procurved, conspicuous, *l.ang.* joined into one conspicuous line, *l.o.p.* short (Text-fig. 123). Genital shield broad and granular. Ventri-anal shield (260μ long × 225μ wide) granular and with transverse lines. All setae are simple.

The chelicera is shown in Text-fig. 124. The brush-like process of the synarthrodial membrane is less than half the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with six stout setae. Tarsus II 139μ (Text-fig. 125), tibia II 83μ.

MALE. Unknown.

LOCALITIES. All the material examined is from one species of beetle, *Gymnopleurus unicolor* Fåhr. The holotype female (1961.7.14.237) and three paratypes (1961.7.14.238–240) collected by C. C. Gowdey (1912–462) at Entebbe, Uganda; three paratypes (1961.7.14.241–243) collected by R. Crawshay (1903–350) at Piet Retief, Transvaal; and one paratype (1961.7.14.244) collected by Dr. Smith (1844–6) in South Africa.

Macrocheles vernalis (Berlese, 1887)

Holostaspis vernalis Berlese, A., 1887, *Acari, Myriopoda et Scorpiones, etc., Fasc.* 45, No. 1.
Macrocheles siculus Oudemans, A. C., 1906, *Ent. Ber.* **2** : 7.

FEMALE. Dorsal shield (700–800μ long × 400–500μ wide) with reticulations entire, and bearing 28 pairs of setae (Text-fig. 126). All setae simple with a few exceptions: the verticals, i1, have their bases in close proximity and are usually pilose distally, and S3, Z3 and J5 are pilose distally. J2 absent.

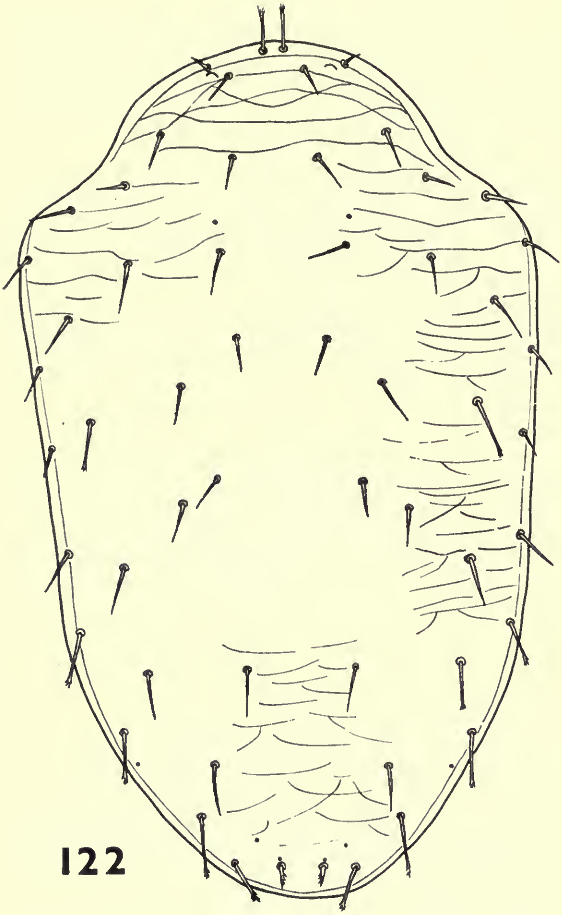
Sternal shield without ornamentation (Text-fig. 127). *L.ang.* short, *l.m.t.* undulating slightly, *l.o.p.* short. Genital shield broad, truncated posteriorly and finely granular. Ventri-anal shield bearing nine simple setae and variable in outline, e.g. in two extreme cases the shield measures 341μ long × 341μ wide (Text-fig. 128), and 253μ long × 209μ wide. The shield is granular with recurved transverse lines. The lengths of the setae vary.

The chelicera is shown in Text-fig. 129. The brush-like process of the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with six setae, all of which are stout and simple. Tarsus II 144μ, tibia II 88μ, all aetae simple.

MALE. Unknown.

DISTRIBUTION. Berlese (1887) described *Holostaspis vernalis* from *Atheucus semipunctatus* at Venezia, Calabria, southwest Italy, and Oudemans (1906) described *Macrocheles siculus* from *Scarabaeus semipunctatus* at Catanta, Sicily. The Museum collections contain specimens from *Scarabaeus semipunctatus* Fabr. in France; from



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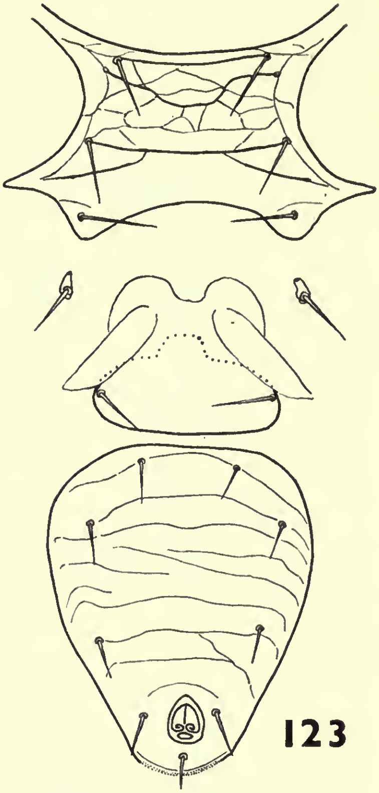

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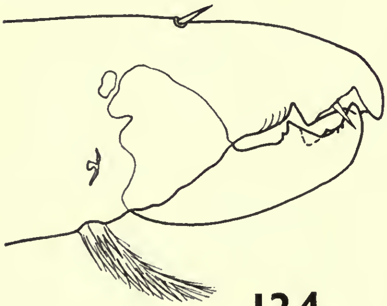

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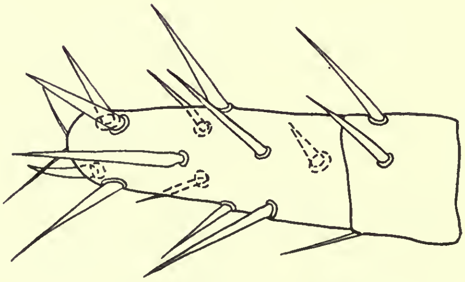

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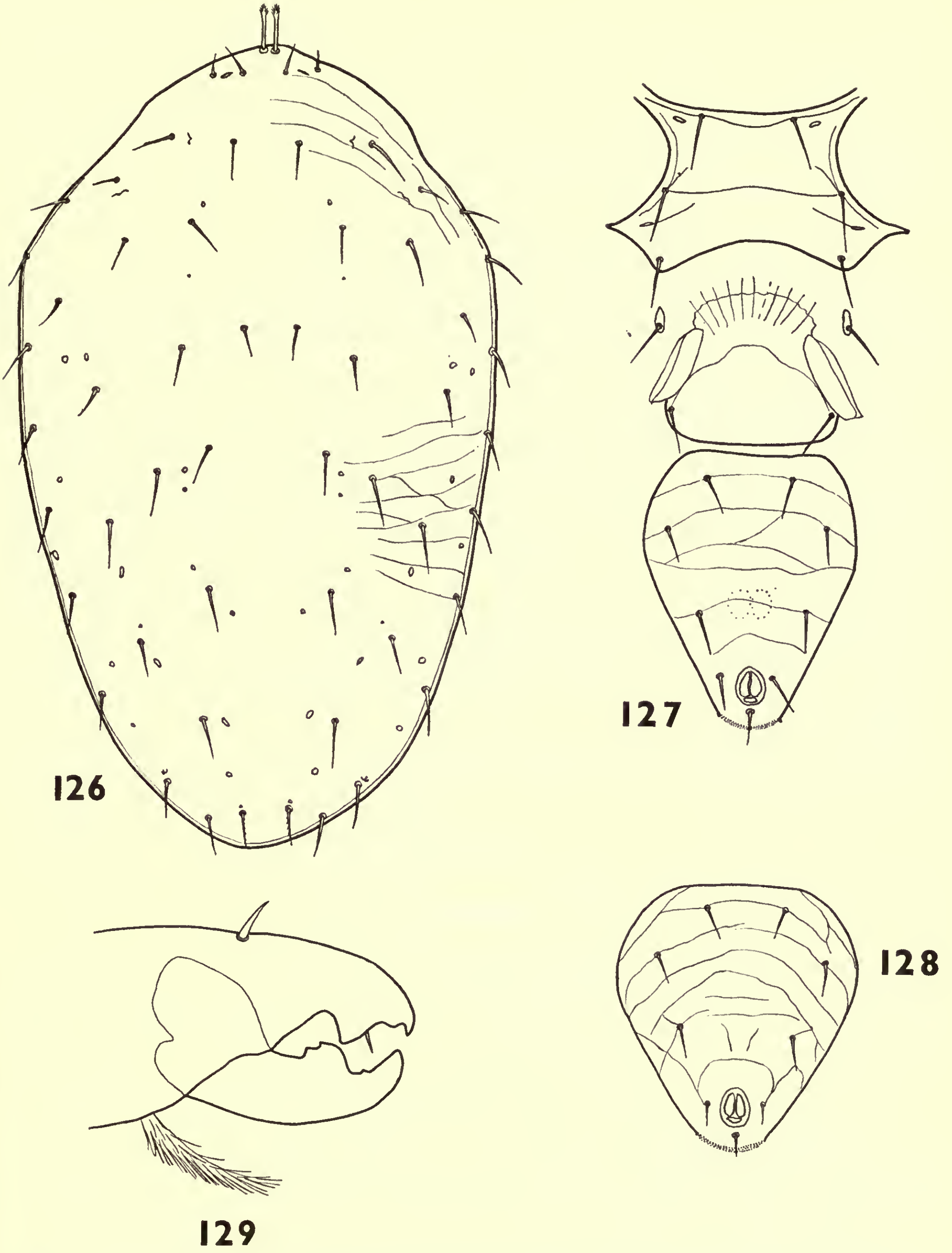
FIGS. 122–125. *Macrocheles transversus* sp. nov., female. Fig. 122, dorsal shield. Fig 123, ventral shields Fig. 124, chelicera. Fig. 125, tarsus II.



FIGS. 126–129. *Macrocheles vernalis* (Berlese), female. Fig. 126, dorsal shield. Fig. 127, ventral shields. Fig. 128, ventri-anal shield. Fig. 129, chelicera.

Scarabaeus sacer L. in France, Romania, Greece, Crete, Turkey, Algeria, Tunisia and China ; from *Scarabaeus pius* Illiger in Armenia ; from *Scarabaeus puncticollis* Latr. in N. Sinai and the Sahara ; from *Scarabaeus gangeticus* Cast. in Aden, Arabia, Liberia, Uganda, Senegal and Nigeria ; from *Scarabaeus cristatus* Fabr. in Arabia ; from *Scarabaeus carinatus* Gebler in Central Asia ; from *Gymnopleurus azureus* Fabr. in Uganda and Angola ; from *Gymnopleurus unicolor* Fåhr. in Uganda ; and from *Gymnopleurus caffer* Fåhr. in South Africa.

Macrocheles verticalis sp. nov.

FEMALE. Dorsal shield (910μ long × 550μ wide) partially reticulated, with characteristic small areas of punctations, and with a conspicuous procurved line medially and bearing 28 pairs of setae (Text-fig. 130). The vertical setae, i1, are elliptical with strongly-serrated edges. Setae i3, i4, i5, z2, z3 and J2 are simple, the remainder are bipectinate.

Sternal shield with punctate areas bordering the *liniae*. *L.m.t.* slightly procurved, *l.arc.* strongly recurved, discontinuous anteriorly, *l.o.p.* reaching a third across the shield (Text-fig. 131). Genital shield broad, truncated posteriorly and with only slight ornamentation. Ventri-anal shield (290μ long × 205μ wide) slightly ovoid with punctate transverse lines. The post-anal seta is pilose distally, the remaining eight are simple.

The chelicera is shown in Text-fig. 132. The brush-like process of the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with six stout strongly bipectinate setae. Tarsus II 205μ (Text-fig. 133), tibia II 100μ. Many of the setae on legs II–IV are bipectinate.

MALE. Unknown.

LOCALITY. A single female (1961.7.14.28) on *Pinotus carolinus* L. from El Zumbador, collected by the Biologia Centrali Americana expedition (1886–90).

MITIS–group

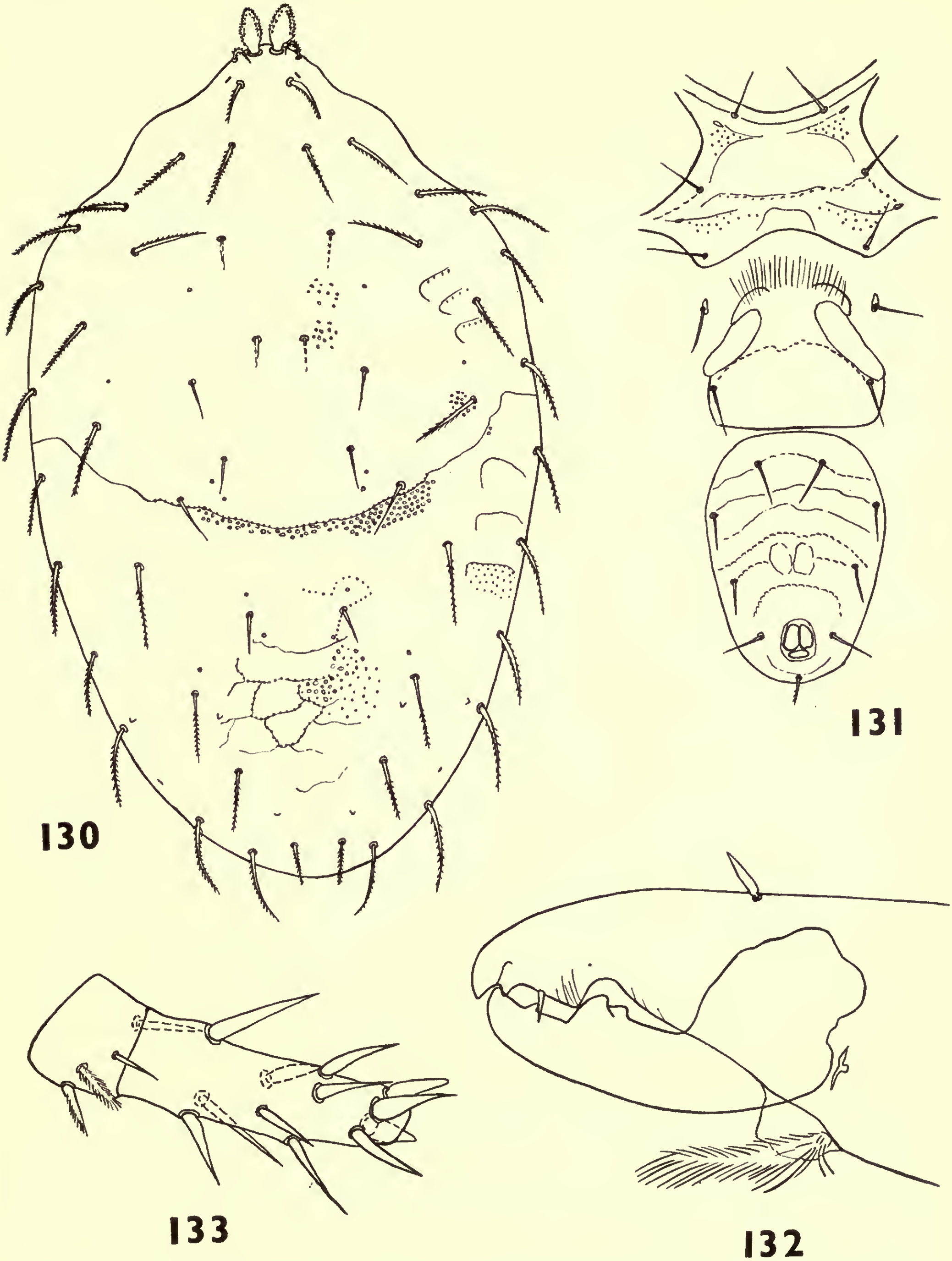
Macrocheles amygdaligera (Berlese), 1918

Holocaeleno (*sic.*) *amygdaligera* Berlese, A., 1918, *Redia* **13** : 177.

FEMALE. Dorsal shield (650μ long × 410μ wide) with small scattered areas of reticulations, faint transverse lines antero-laterally, and bearing 29 pairs of setae (Text-fig. 134). Setae i1, the verticals, are stout and thorn-like, r4 are the longest (c. 65μ) and all are simple with the exception of the finely pilose J5. J2 present.

Sternal shield finely granular, posterior margin strongly concave (Text-fig. 135). *L.m.t.* strongly procurved, *l.arc.* strongly recurved, continuous in some specimens, broken in others. Genital shield truncated posteriorly, finely granular. Ventri-anal shield (225μ long × 185μ wide) ovoid, finely granular and with transverse lines in the anterior half. The paranals are the longest of the nine ventri-anal setae.

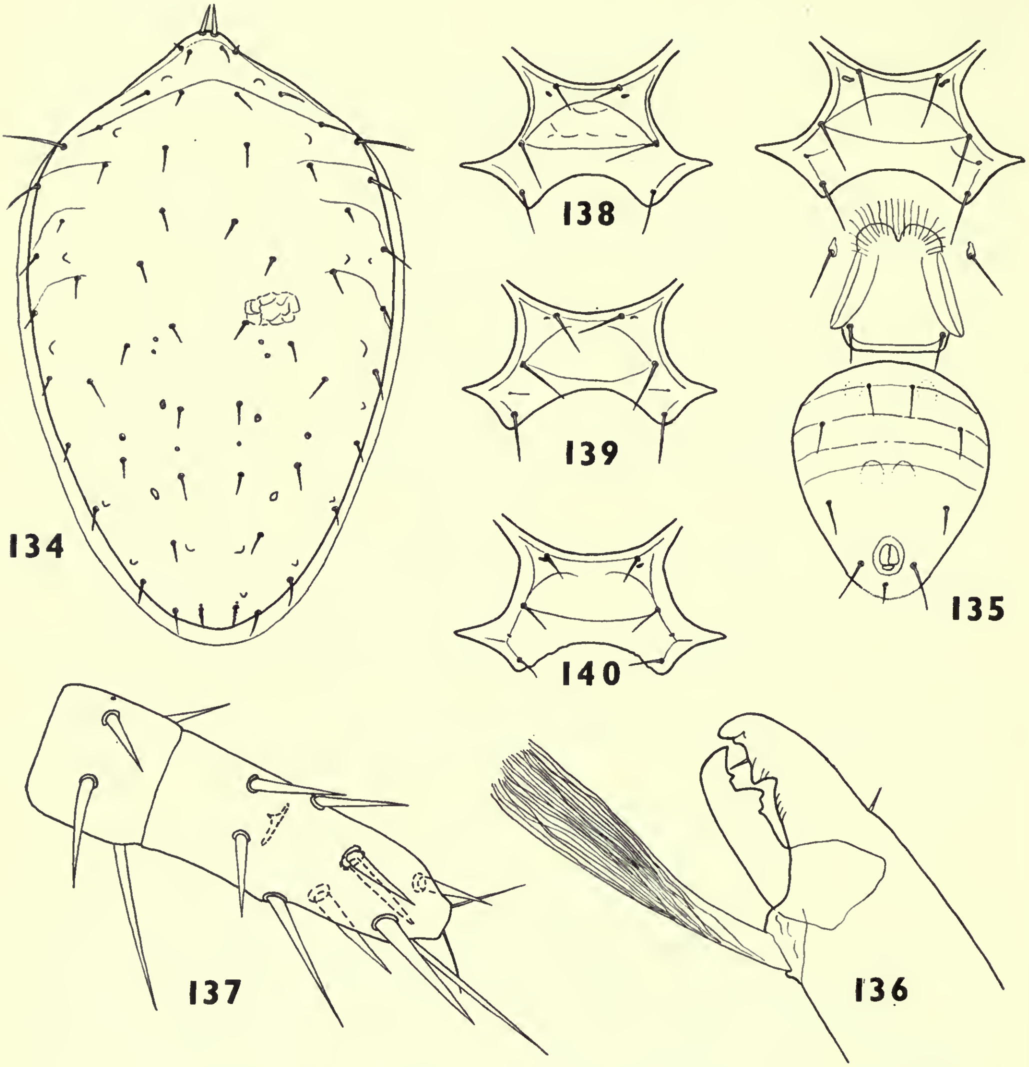
The chelicera is shown in Text-fig. 136. The brush-like process of the synarthrodial membrane is one and a half times as long as the movable digit. Six rows of deutosternal teeth.



FIGS. 130–133. *Macrocheles verticalis* sp. nov., female. Fig. 130, dorsal shield. Fig. 131, ventral shields. Fig. 132, chelicera. Fig. 133, tarsus II.

Genu IV with seven stout setae, of which the dorsal series is slightly pilose, remaining three simple. Tarsus II 125μ (Text-fig. 137), tibia II 95μ.

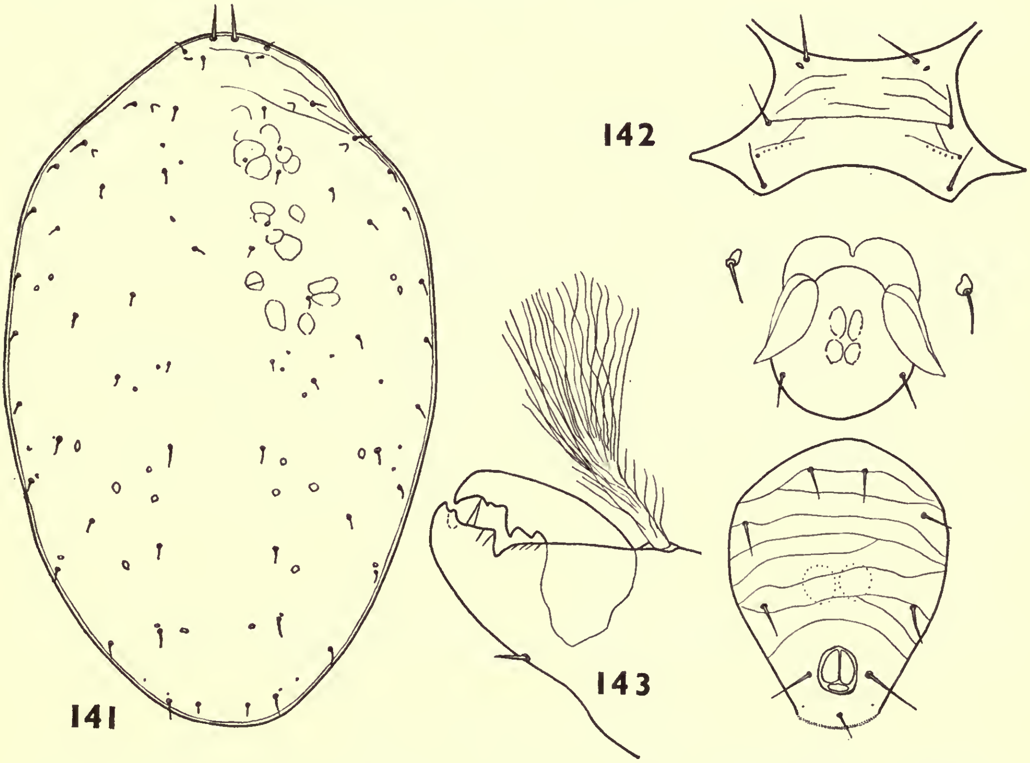
There is considerable variation in the ornamentation and outline of the sternal shield (Text-figs. 138–140), and in the outline and measurement of the ventri-anal shield.



Figs. 134–140. *Macrocheles amygdaligera* (Berlese), female. Fig. 134, dorsal shield. Fig. 135, ventral shields. Fig. 136, chelicera. Fig. 137, tarsus II. Figs. 138–140, sternal shields.

Male. This sex is described by Berlese (1918): we have not examined fresh material.

Distribution. Berlese (*loc. cit.*) examined many specimens of both sexes on *Phanaeus splendidulus* Fabr. from Buenos Aires, Argentina. The present collection contains many females on *Phanaeus imperator* Chevr., *Phanaeus horus* Waterh. and *Phanaeus menelas* Cast. in Argentina ; on *Phanaeus lancifer* L. in British and French Guiana ; on *Phanaeus amethystinus* Harold in Guatemala ; on *Phanaeus faunus* Fabr. in the Lower Amazons ; on *Phanaeus telamon* Erichs. in Panama ; on *Phanaeus bonariensis* Gory, *Phanaeus palaeno* Blanch. and *Phanaeus ensifer* Germ. in Paraguay ; on *Phanaeus igneus* McLeay in South Carolina ; on *Phanaeus sulcatus* Drury in Jamaica ; and on *Phanaeus lancifer* labelled " S. America ".



Figs. 141–143. *Macrocheles dubius* sp. nov., female. Fig. 141, dorsal shield. Fig. 142, ventral shields. Fig. 143, chelicera.

Macrocheles dubius sp. nov.

Female. Dorsal shield ($1{,}111\mu$ long × 726μ wide) finely granular with a few small scattered areas of reticulation, conspicuous pores, and bearing 29 pairs of setae (Text-fig. 141). The verticals, i1, are slender and thorn-like, their bases about two diameters apart. J5 are slightly palmate, the remaining setae fine and simple. Setae J2 present.

Sternal shield granular, faint traces of reticulation (Text-fig. 142). *L.m.t.* straight, *l.arc.* strongly recurved, discontinuous anteriorly. Genital shield semicircular posteriorly, finely granular, four circular areas medially. Ventri-anal shield ovoid, finely granular, anterior margin strongly convex, conspicuous transverse lines. The paranals are the longest of the nine ventri-anal setae.

The chelicera is shown in Text-fig. 143. The brush of setae on the synarthrodial membrane is one and a half times as long as the movable digit. Six rows of deutosternal teeth.

Genu IV with seven stout simple setae. Tarsus II 202μ, tibia II 152μ.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.3) and five paratypes (1961.7.14.4–8) on *Phanaeus splendidulus* Fabr. from Argentina, bearing labels of the Fry collection (1905–100) and Col. Taylor (1906–199).

Macrocheles floridanus sp. nov.

FEMALE. Dorsal shield (415μ long × 280μ wide) irregular in outline, weakly sclerotized with very conspicuous pores, and with 27 pairs of setae (Text-fig. 144). Setae s2 and i2 missing in the unique specimen. There is an extra unpaired seta posterior to left i5. J2 present. Setae i1 are thorn-like and J5 slightly pilose ; the remainder are simple with S4 and S5 the longest (c. 21μ), the remainder are very short (up to 9μ).

Sternal shield finely granular. *L.m.t.* apparently absent, *l.arc.* strongly recurved, continuous (Text-fig. 145). Genital shield flask-shaped, almost semicircular posteriorly, granular. Ventri-anal shield (110μ long × 90μ wide) ovoid with a slight concavity on the left margin, and bearing only seven simple setae.

The chelicera is shown in Text-fig. 146. The brush of setae on the synarthrodial membrane is almost twice the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with seven simple setae. Tarsus II (Text-fig. 147) 88μ, tibia II 63μ.

MALE. Unknown.

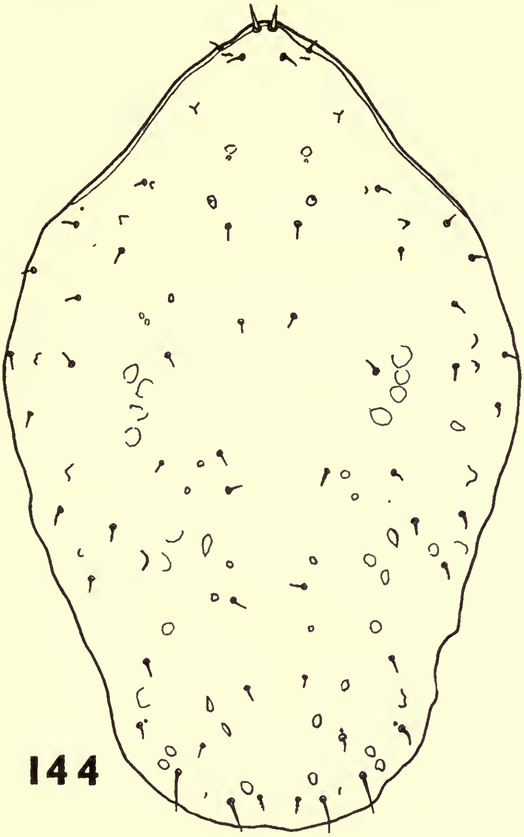
LOCALITY. A single female (1961.7.14.54) on *Deltochilum orbiculare* Lansb., collected in 1931 by G. Klug at SE. Columbia, Florida, U.S.A.

Macrocheles grandis sp. nov.

FEMALE. Dorsal shield (930μ long × 620μ wide) with only a few areas of faint reticulation and bearing 29 pairs of setae (Text-fig. 148). Verticals, i1, stout and simple, their bases two diameters apart ; setae i4, i5, z2, z3, J2, J3 and J5 short (c. 18–25μ), simple and fine ; remaining setae longer (up to 135μ) and sparsely pilose.

Sternal shield finely granular, posterior margin strongly concave (Text-fig. 149). *L.m.t.* straight, pronounced, *l.arc.* strongly recurved, discontinuous anteriorly. Genital shield slightly concave posteriorly, granular. Ventri-anal shield (310μ long

FIGS. 144–147. *Macrocheles floridanus* sp. nov., female. Fig. 144, dorsal shield. Fig. 145, ventral shields. Fig. 146, chelicera. Fig. 147, tarsus II.



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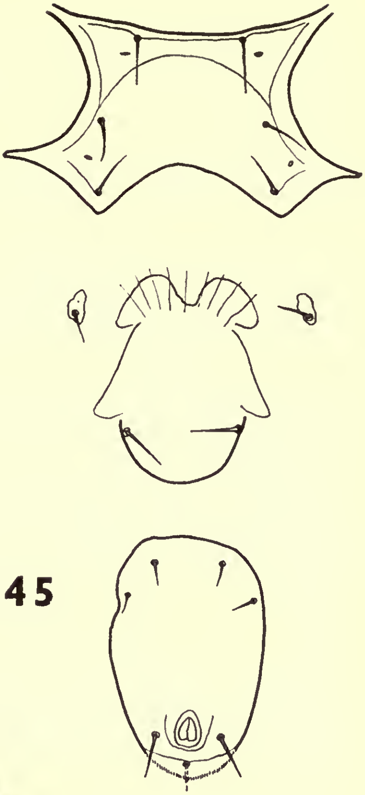

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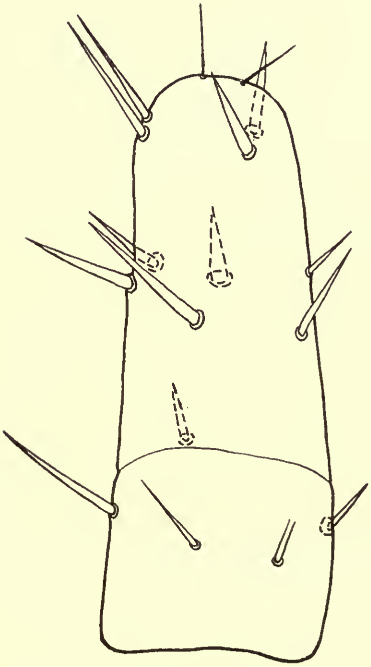

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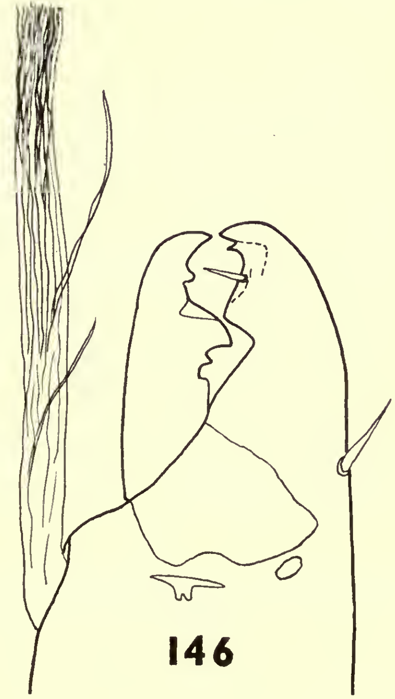
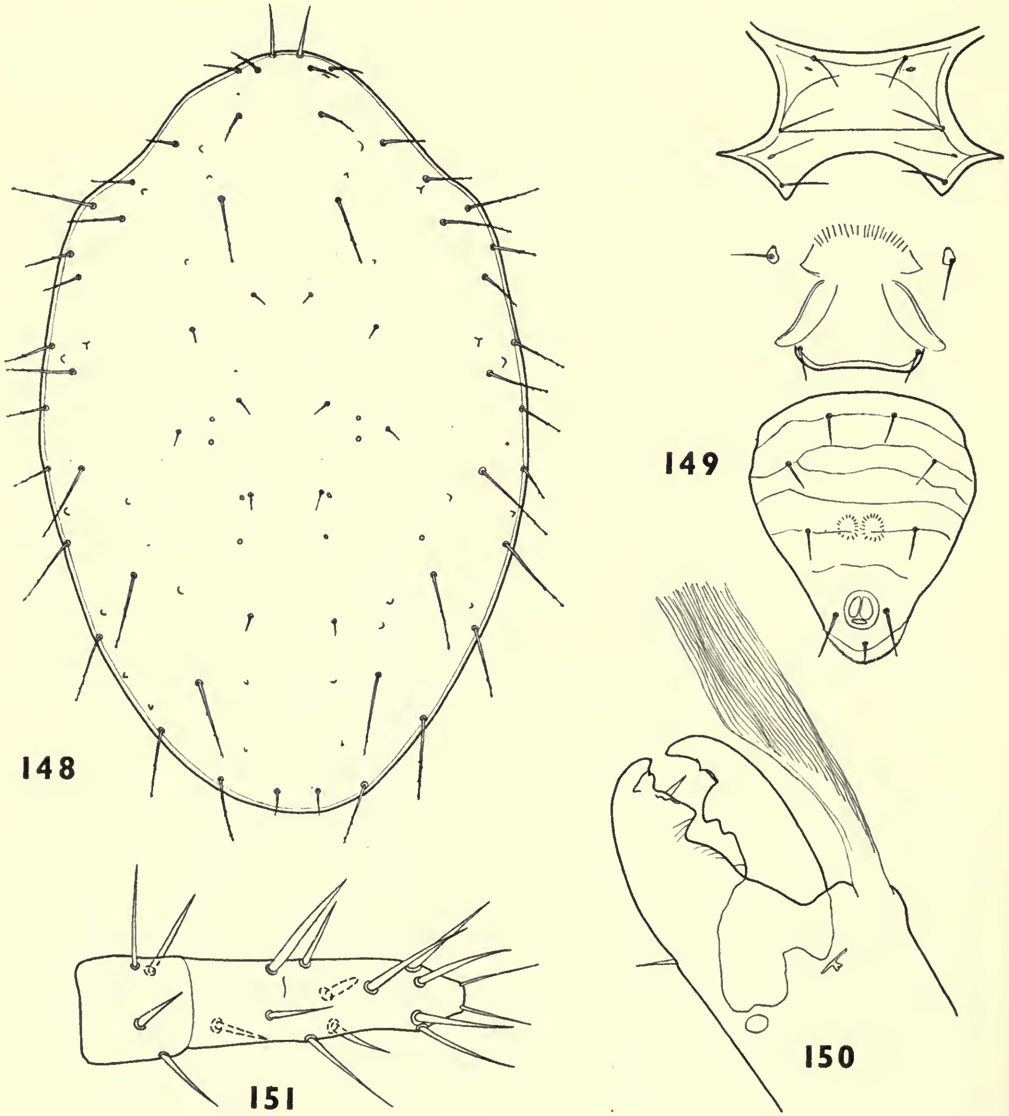


146

× 235μ wide) granular, with transverse reticulations. The paranals are the longest of the nine ventri-anal setae.

The chelicera is shown in Text-fig. 150. The brush of setae on the synarthrodial membrane is one and a half times as long as the movable digit. Six rows of deutosternal teeth.

Genu IV with seven stout setae; ad_1 is conspicuously long and slightly pilose, remainder simple. Tarsus II 203μ (Text-fig. 151), tibia II 130μ.



Figs. 148–151. *Macrocheles grandis* sp. nov., female. Fig. 148, dorsal shield. Fig. 149, ventral shields. Fig. 150, chelicera. Fig. 151, Tarsus II.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.29) and one paratype (1961.7.14.30) on *Deltochilum lobipes* Bates, purchased from Dyson (1845–123) and collected at Honduras.

Macrocheles phanaei Berlese, 1916

Holocaeleno (*sic.*) *mitis* Berl. var. *phanaei* Berlese, A., 1916, *Redia* **12** : 154.

FEMALE. Dorsal shield (473μ long × 308μ wide) with 29 pairs of setae and conspicuous pores, granular and with pronounced transverse lines anteriorly (Text-fig. 152). The verticals, i1, are stout and spinose, all other setae are very short (c. 10μ) and simple. J2 present.

Sternal shield broad, strongly granular, posterior margin concave (Text-fig. 153). *L.m.t.* distinct, only slightly concave, *l.arc.* arising from the lateral margin of the shield, discontinuous. Ventri-anal shield (165μ long × 154μ wide) finely granular, reticulated and bearing nine simple setae of which the paranals are the longest.

The chelicera is shown in Text-fig. 154. The brush of setae on the synarthrodial membrane is almost twice the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with seven simple setae. Tarsus II 88μ, tibia II 55μ.

MALE. Unknown.

DISTRIBUTION. The type locality is " super *Phanaeus perspicillatus* ; Ecuador ". We have examined additional specimens on *Phanaeus splendidulus* F. from Ecuador : one in the Fry collection (1905–100) and three collected by Col. Taylor (1906–199).

Macrocheles scapularis sp. nov.

FEMALE. Dorsal shield (570μ long × 370μ wide) finely granular, completely devoid of all ornamentation and bearing 29 pairs of simple setae (Text-fig. 155). The verticals, i1, are thorn-like. With the exception of r4 which are c. 65μ long, all other dorsal setae are c. 9μ long. Seta J2 present.

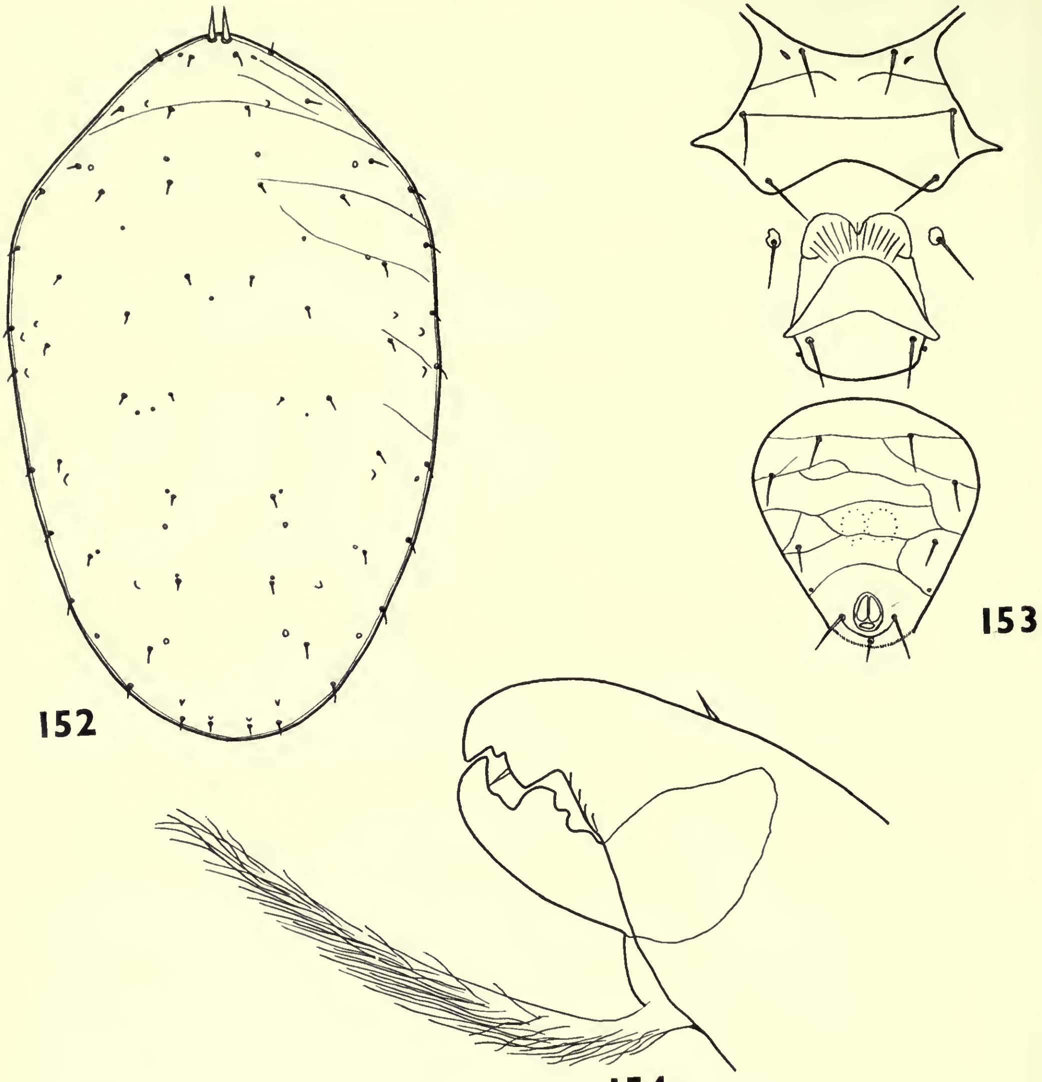
Sternal shield with very fine granulations centrally, becoming coarser towards the margins. Posterior margin strongly concave (Text-fig. 156). *L.m.t.* apparently absent, *l.arc.* strongly recurved, discontinuous anteriorly. Sternal setae long. Genital shield finely granular. Ventri-anal shield (185μ long × 155μ wide) ovoid, granular and devoid of ornamentation and bearing nine simple setae of which the paranals are the longest.

The chelicera is shown in Text-fig. 157. The brush- like process of the synarthrodial membrane is slightly longer than the movable digit. Six rows of deutosternal teeth.

Genu IV with seven simple setae. Tarsus II with very slender setae (Text-fig. 158), 88μ long, tibia II 65μ.

MALE. Unknown.

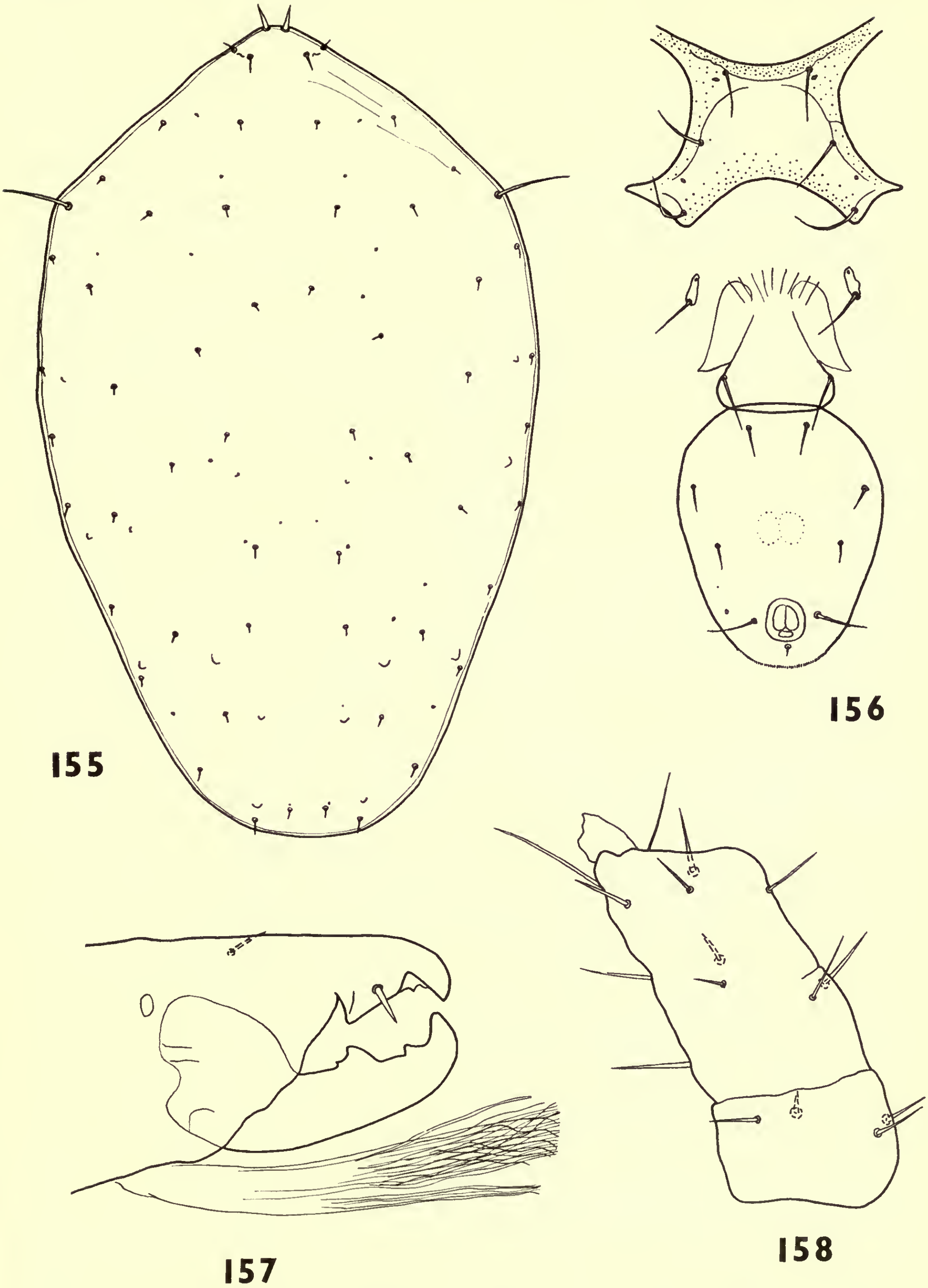
LOCALITY. A single female (1961.7.14.23) on *Deltochilum lobipes* Bates in the Nevinson collection (1918–14) from " North America ".



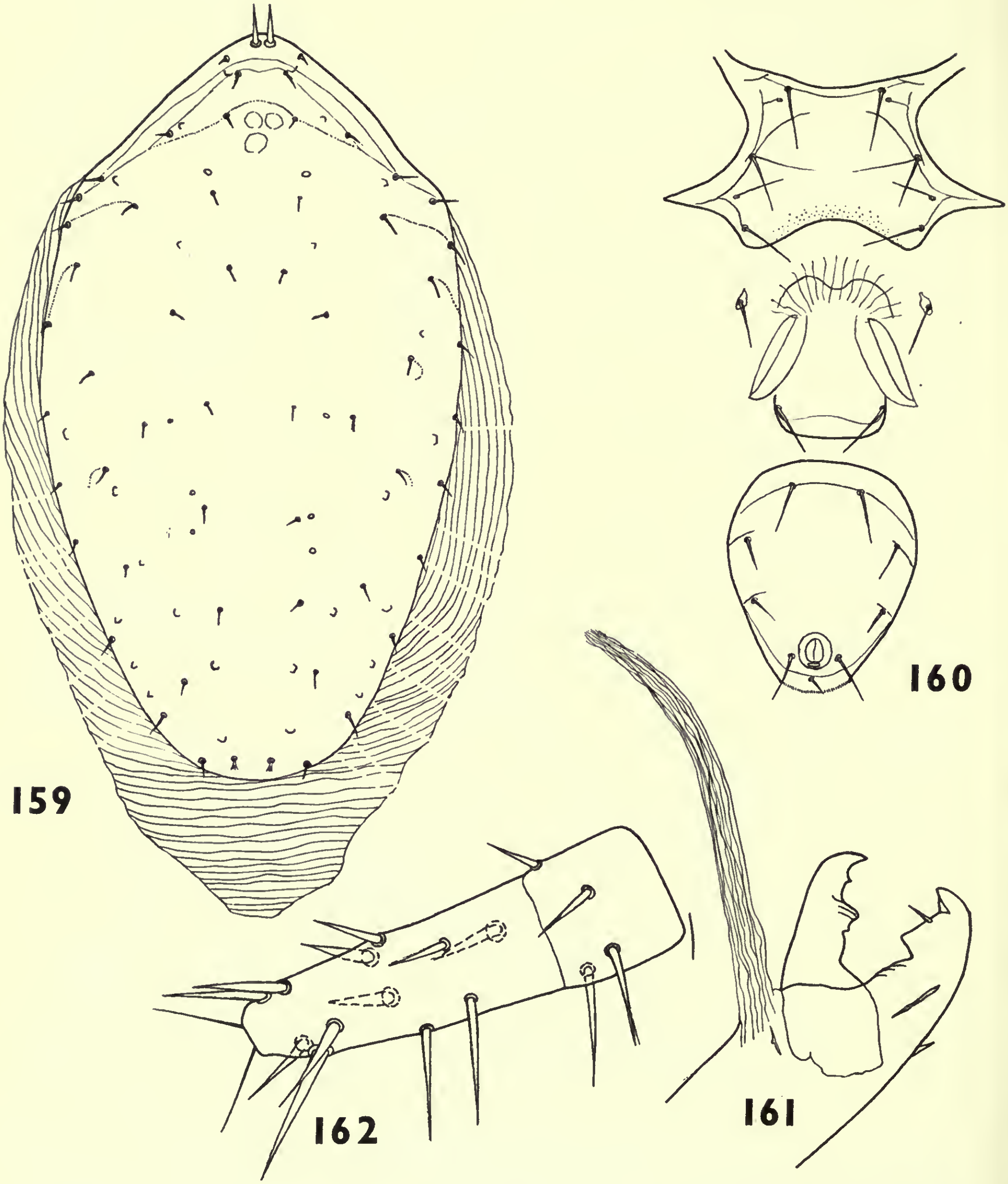
Figs. 152–154. *Macrocheles phanaei* Berlese, female. Fig. 152, dorsal shield. Fig. 153, ventral shields. Fig. 154, chelicera.

Macrocheles turki sp. nov.

Female. Dorsal shield (620μ long × 390μ wide) with 29 pairs of setae and conspicuous pores, but the only ornamentation is a few transverse lines anteriorly. Surrounding the dorsal shield posterior to setae r4 is a broadening sclerotized strip of cuticle (Text-fig. 159). With the exception of J5, which are short and palmate, and i1, which are thorn-like, all setae are simple and short (c. 15μ). J2 present.



FIGS. 155–158. *Macrocheles scapularis* sp. nov., female. Fig. 155, dorsal shield. Fig. 156, ventral shields. Fig. 157, chelicera. Fig. 158, tarsus II.



Figs. 159–162. *Macrocheles turki* sp. nov., female. Fig. 159, dorsal shield. Fig. 160, ventral shields. Fig. 161, chelicera. Fig. 162, tarsus II.

Sternal shield finely granular, posterior margin concave (Text-fig. 160). *L.m.t.* slightly procurved, discontinuous medially, *l.arc.* strongly recurved, also discontinuous. Genital shield narrow and granular. Ventri-anal shield (185μ long × 160μ wide) ovoid, finely granular; the only ornamentation being a faint recurved line anteriorly. The paranals and the anterior pair are the longest of the ventri-anal setae.

The chelicera is shown in Text-fig. 161. The brush of setae on the synarthrodial membrane is twice the length of the movable digit. Six rows of deutosternal teeth.

Genu IV with seven simple setae, pd_2 stoutest. Tarsus II (Text-fig. 162) 134μ, tibia II 82μ.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.255) and one paratype (1961.7.14.256) on *Phanaeus telamon* Erichs., collected on the Biologia Centrali Americana expedition (1886–90) at Volcan de Chiriqui, Panama.

This species is named after Dr. F. A. Turk.

BREGETOVAE–group

Macrocheles austroamericanus sp. nov.

FEMALE. Dorsal shield (950μ long × 540μ wide) finely granular, with very faint areas of reticulation, and bearing 29 pairs of setae (Text-fig. 163). Setae r1 are simple but all the other setae are pilose to a certain degree, viz.: i1 are pilose on their outer margins only, i4, i5, z2, z3, J2 and J3 are scarcely pilose, whereas the remainder are more markedly so.

Sternal shield granular, coarsely along the concave posterior margin (Text-fig. 164). *L.m.t.* almost straight, slight undulation, *l.arc.* strongly recurved, short on each side, *l.o.p.* curving up to meet *l.m.t.* Genital shield granular, truncated posteriorly. Ventri-anal shield (330μ long × 225μ wide) narrow, slightly concave sides and with transverse lines.

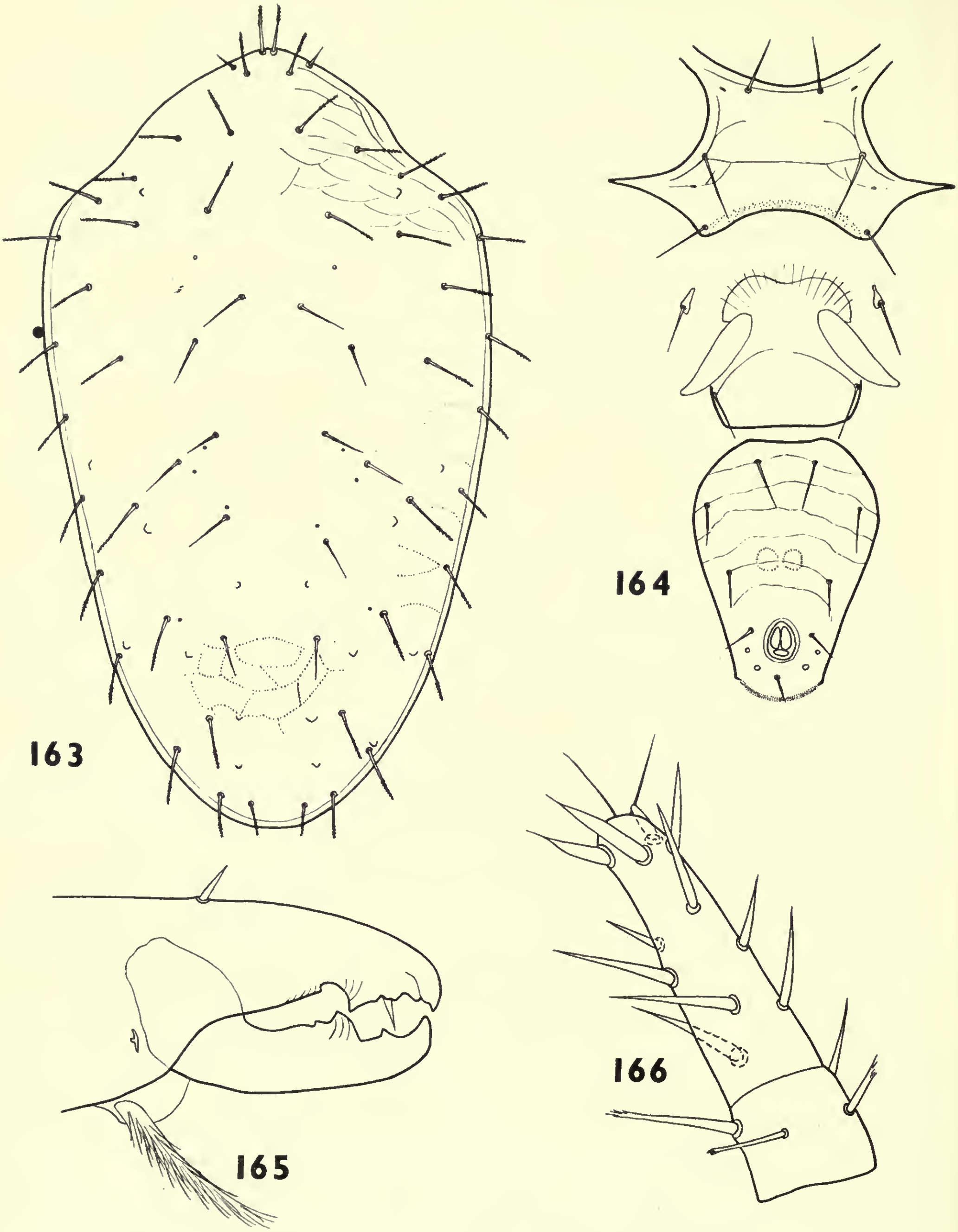
The chelicera is shown in Text-fig. 165. The brush of setae-like processes on the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with six stout setae, all of which are pilose. Tarsus II 202μ (Text-fig. 166), tibia II 126μ.

MALE. Unknown.

LOCALITIES. The holotype female (1961.7.14.31) and over a dozen paratypes (1961.7.14.32–42) on *Phanaeus imperator* Chev. from Nanahua, Paraguayan Chaco, Paraguay, collected by G. S. Carter (1928–50); and further paratypes from: *Ontherus sulcator* Fabr., Rio Salado, Argentina; *Chalcocopris hesperus* Oliv., Rio de Janeiro, Brazil; *Phanaeus kirbyi* Vigors, Chapada, central Brazil; *Phanaeus lancifer* L., Essequibo River, Moraballi Creek, British Guiana; *Phanaeus scintillans* Bates, Temascaltapec, Mexico; and *Phanaeus telamon* Erichs., also from Mexico.

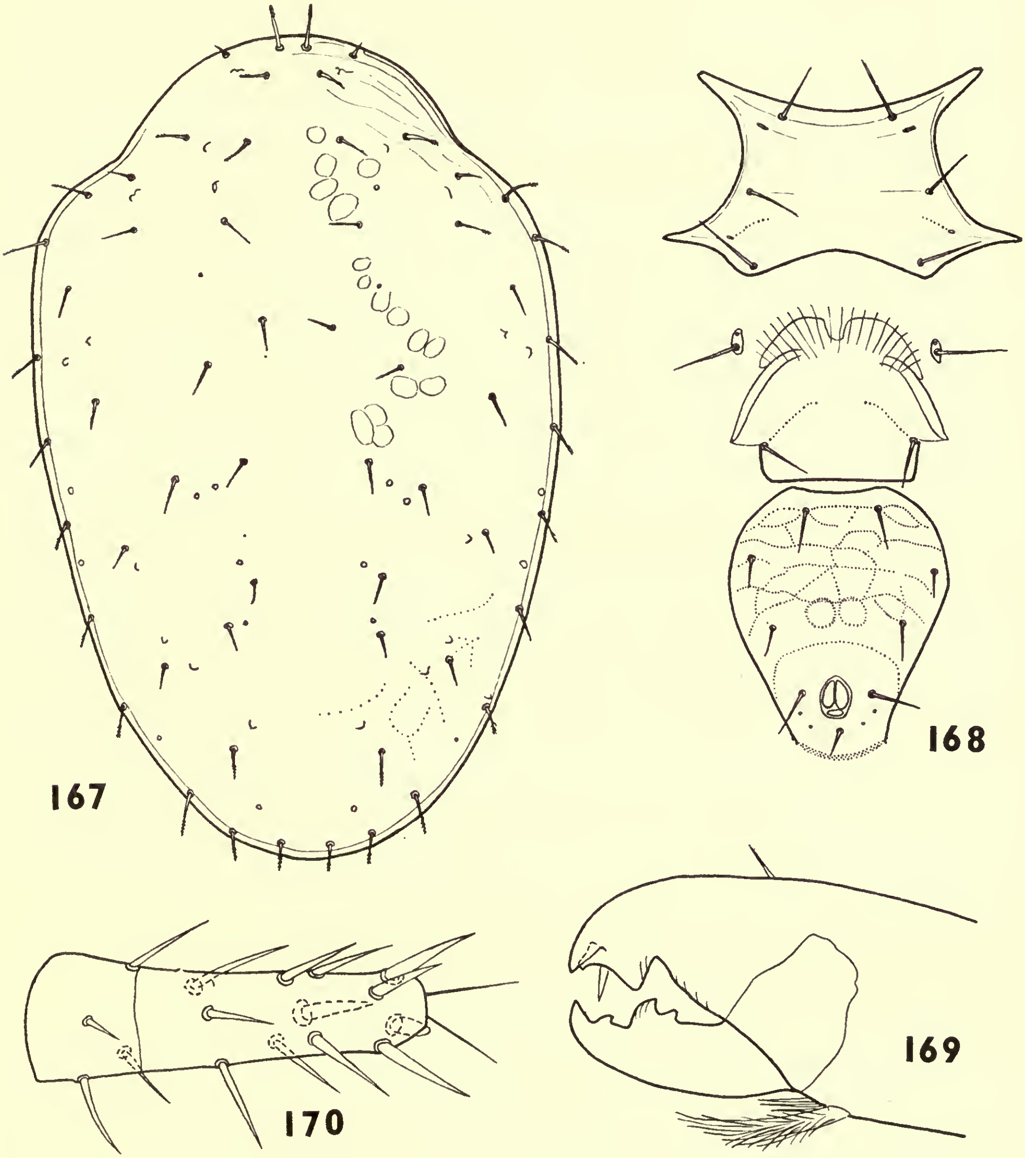
This species appears to be closely related to *Macrocheles cordiger* (Berlese, 1888) and to *M. spinosus* Berl., 1918, but differs in the form and chaetotaxy of the dorsal shield.



FIGS. 163–166. *Macrocheles austroamericanus* sp. nov., female. Fig. 163, dorsal shield. Fig. 164, ventral shields. Fig. 165, chelicera. Fig. 166, tarsus II.

Macrocheles brasiliensis sp. nov.

FEMALE. Dorsal shield (880μ long × 540μ wide) with only very faint traces of granulation, and bearing 29 pairs of setae (Text-fig. 167). Setae r1, r3, s5, i4, i5, z2, z3, Z1, Z2, J2 and J3 are simple, the remainder are finely pilose distally on one or both margins. The verticals, i1, are separated by twice the diameter of their bases.



FIGS. 167–170. *Macrocheles brasiliensis* sp. nov., female. Fig. 167, dorsal shield. Fig. 168, ventral shields. Fig. 169, chelicera. Fig. 170, tarsus II.

Sternal shield granular, *l.m.t.* incomplete, *l.ang.* and *l.o.p.* very short (Text-fig. 168). Genital shield broad, truncated posteriorly. Ventri-anal shield (280μ long × 240μ wide) slightly concave anteriorly, granular, and with fine punctate transverse lines. The nine setae are simple.

The chelicera is shown in Text-fig. 169. The brush-like process of the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with seven setae all of which are finely pilose distally. Tarsus II (Text-fig. 170) 185μ, tibia II 125μ.

MALE. Unknown.

LOCALITY. The holotype female (1961.7.14.245) and one paratype (1961.7.14.246) on *Phanaeus bellicosus* Oliv. in the Nevinson collection (1918–14) from Sta. Catherina, Brazil.

Macrocheles bregetovae sp. nov.

FEMALE. Dorsal shield (1,050μ long × 630μ wide) with faint areas of reticulation around the edges and bearing 29 pairs of setae (Text-fig. 171). Setae i5, z3 and Z1 are simple, the remainder are pilose in at least their distal thirds. The verticals, i1, are separated by a little less than the diameter of their bases. J2 present.

Sternal shield finely granular. *L.m.t.* slightly procurved, *l.arc.* strongly recurved, discontinuous anteriorly (Text-fig. 172). Genital shield broad, truncated posteriorly. Ventri-anal shield (300μ long × 250μ wide) finely granular, with faint transverse lines. The post-anal seta is shorter than the other eight on the ventri-anal shield and is slightly pectinate terminally : some of the remainder show traces of pectination.

The chelicerae are shown in Text-fig. 173. The setae-like process of the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with six setae, all of which are strongly pilose in their distal halves. Tarsus II 205μ (Text-fig. 174), tibia II 130μ.

MALE. Unknown.

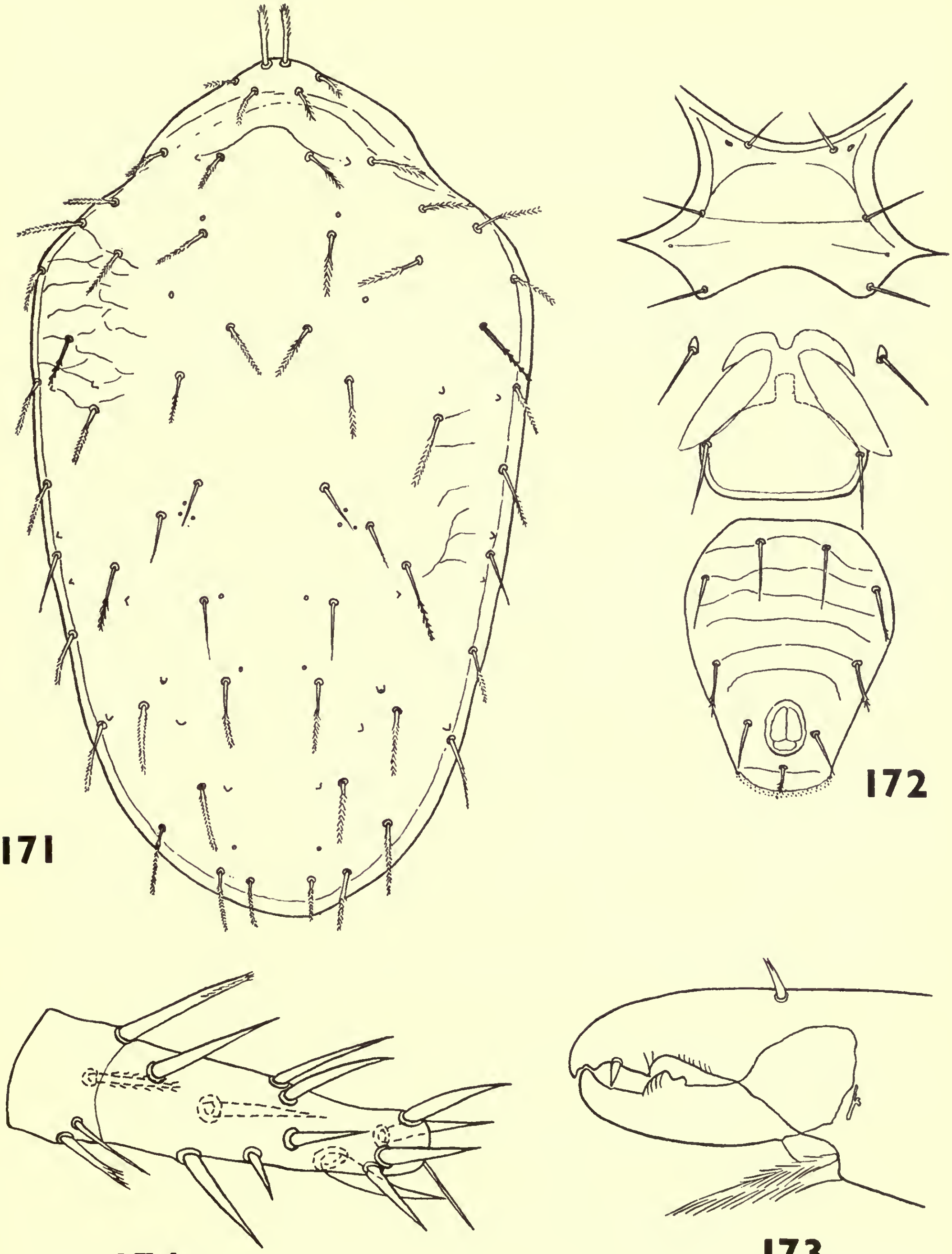
LOCALITIES. The holotype female (1961.7.14.9) and ten paratypes (1961.7.14.10–19) on *Pinotus carolinus* L. from El Zumbador, and one paratype (1961.7.14.21) also on *Pinotus carolinus* from Zapote, all Guatemala, collected by Biologia Centrali Americana (1886–90) ; one paratype (1961.7.14.20) on *Phanaeus wagneri* Harold from Guatemala ; and one paratype (1961.7.14.22) on *Phanaeus bonariensis* Gory from Asuncion, Paraguay, collected by E. G. Kent (1925–262).

This species is named after Dr. Nina Bregtova.

Macrocheles filipponii sp. nov.

FEMALE. Dorsal shield (1,060μ long × 670μ wide) with areas of granulation and faint sparse reticulations around the margin (Text-fig. 175). All the 29 pairs of dorsal setae are strongly bipectinate ; the verticals, i1, have their bases less than one diameter apart ; r1 and J5 are the shortest. The setae on the interscutal membrane surrounding the dorsal shield are also bipectinate. J2 present.

Sternal shield granular, with punctate areas (Text-fig. 176). *L.m.t.* almost straight, *l.arc.* strongly recurved, discontinuous anteriorly. Genital shield broad, truncated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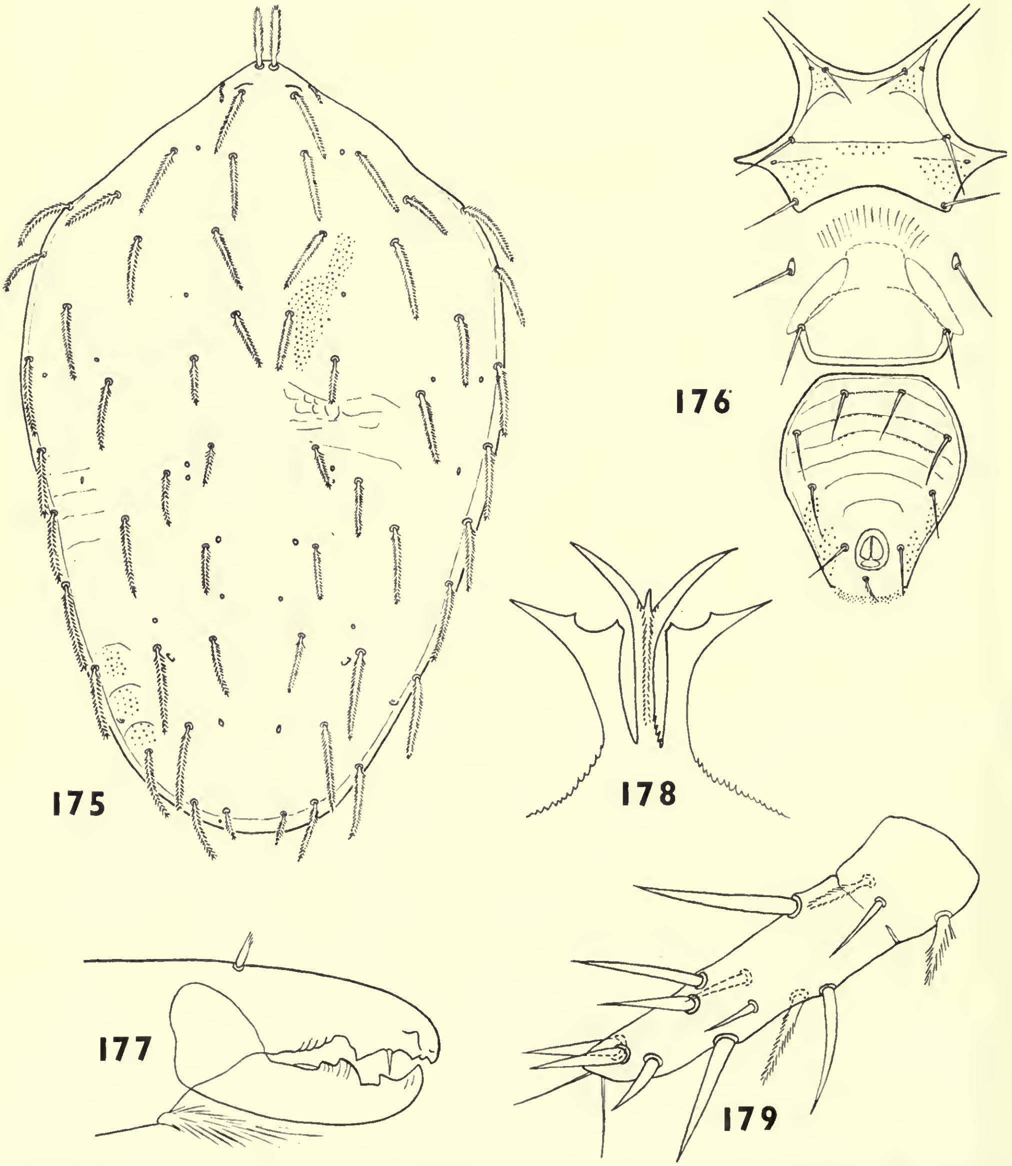
FIGS. 171–174. *Macrocheles bregetovae* sp. nov., female. Fig. 171, dorsal shield. Fig. 172, ventral shields. Fig. 173, chelicera. Fig. 174, tarsus II.

posteriorly, finely granular. Ventri-anal shield (320μ long × 270μ wide) with anterior margin straight, finely granular, and with recurved transverse lines bordered with fine areolations. The post-anal seta is slightly pilose and is the shortest of the nine setae on the ventri-anal shield.

The brush-like process of the synarthrodial membrane of the chelicera is short (Text-fig. 177). The tectum is shown in Text-fig. 178. Six rows of deutosternal teeth.



Figs. 175–179. *Macrocheles filipponii* sp. nov., female. Fig. 175, dorsal shield. Fig. 176, ventral shields Fig. 177, chelicera. Fig. 178, tectum. Fig. 179, tarsus II.

Chaetotaxy of legs : Leg I : tarsus with very fine simple setae, remaining segments with majority of setae stouter and pectinate. Leg II : tarsus (237μ) with thorn-like setae, some of which are pectinate (Text-fig. 179), tibia (155μ) and remaining segments with most setae pectinate, genu and femur each with a single short broad bipectinate seta dorsally. Leg III with setae less stout than on leg IV, majority pectinate to some degree, femoral setae noticeably stoutest. Genu IV with six strongly pectinate setae, remaining setae mostly pectinate, femur with two stouter setae dorsally.

MALE. Unknown.

LOCALITIES. The holotype female (1961.7.14.1) on *Pinotus carolinus* Fabr. in the Pittier collection (1895–155) from Costa Rica ; and one paratype (1961.7.14.2) on *Eurysternus claudicans* Kirsch collected by the Biologia Centrali Americana expedition (1886–90) at Coban, Vera Paz, Guatemala.

This species is named after Dr. A. Filipponi.

Macrocheles hirsutissima (Berlese, 1910)

Holostaspella hirsutissima Berlese, A., 1910, *Redia* **6** : 248.

FEMALE. Dorsal shield (940μ long × 570μ wide) with a characteristic pattern of depressions, ridges and punctations, and bearing 29 pairs of setae (Text-fig. 180). Setae i1 are broad and flat with strongly pectinate margins ; setae i3–i5 and z2 are simple or with only occasional pectinations. The remaining setae are all strongly bipectinate and the lateral interscutal membrane bears on each side of the dorsal shield a row of 20 similar setae. There is a band of sclerotized cuticle around the posterior margin of the dorsal shield. J2 present.

Sternal shield well ornamented with reticulations and areolate areas. *L.m.t.* undulated, *l.ang.* recurved (Text-fig. 181). Genital shield truncated posteriorly, slightly concave, and with areolations. Ventri-anal shield (330μ long × 280μ wide) irregularly ovoid in outline, with punctate transverse lines and areolations especially in the posterior half. The nine setae are simple.

The chelicera is shown in Text-fig. 182. The chelical brush is short. Six rows of deutosternal teeth.

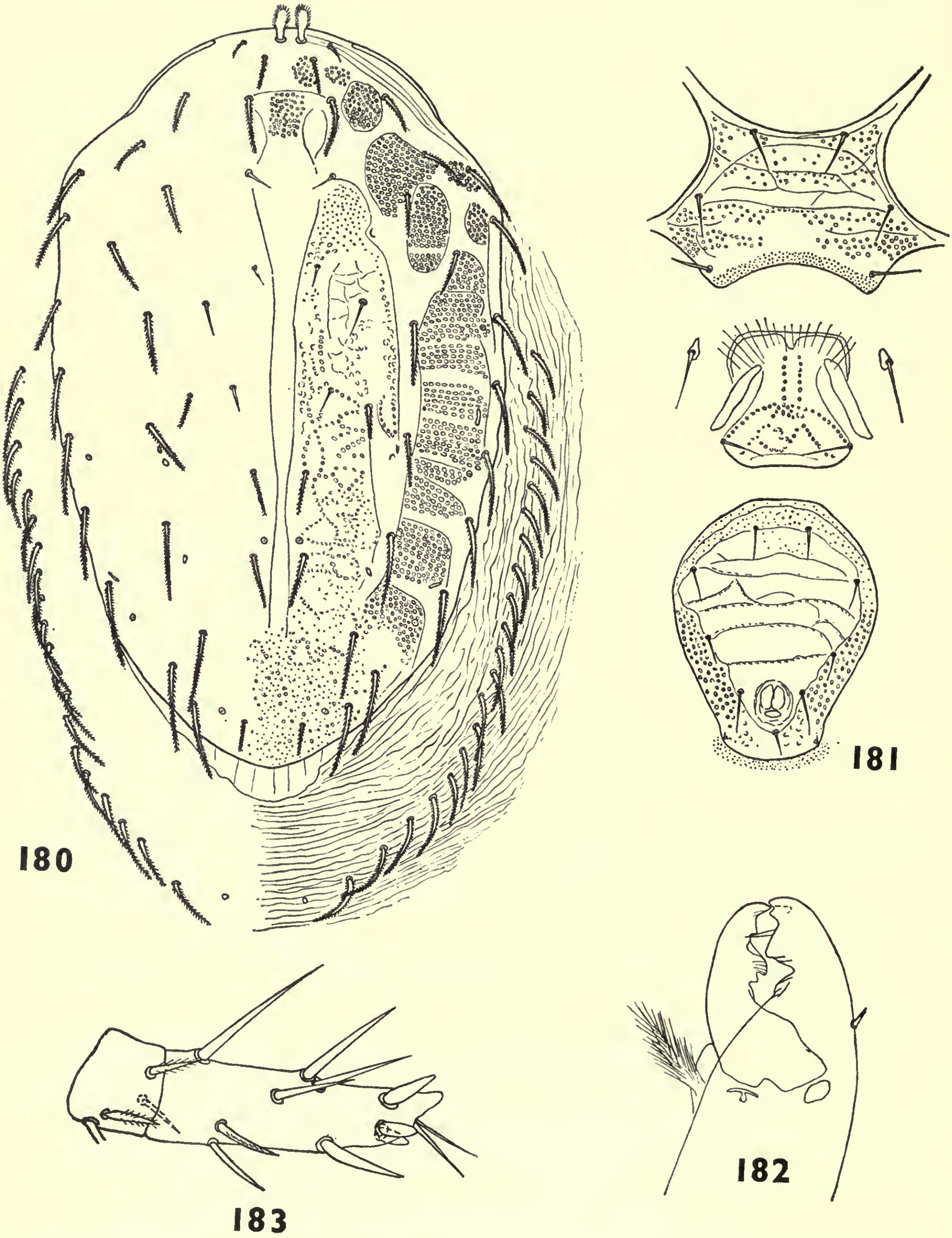
Genu IV with seven setae which, although damaged in the only specimen we have, appear to be pilose distally. Tarsus II 185μ (Text-fig. 183), tibia II 145μ.

MALE. Unknown.

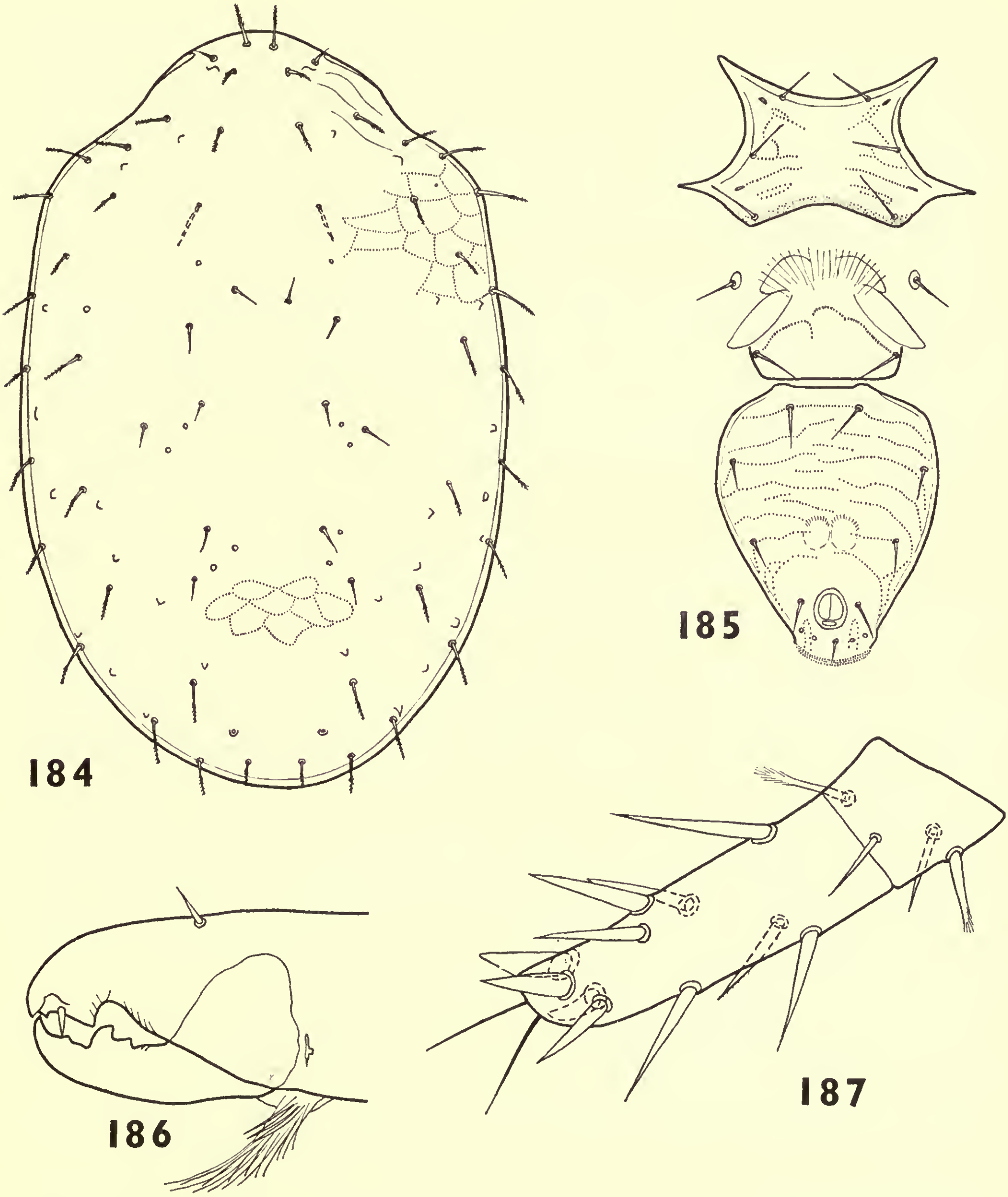
DISTRIBUTION. Berlese (1910) described specimens on *Copris bituberculatus* in Texas and *Copris carolina* in " America boreale ". We have figured a single female on *Phanaeus lancifer* L., collected at Moraballi Creek, Essequibo River, British Guiana, by the Oxford University Expedition (1929–435).

Macrocheles pegazzanae sp. nov.

FEMALE. Dorsal shield (952–1,235μ long × 591–785μ wide) entirely covered by a very fine punctate reticulation and bearing 29 pairs of setae (Text-fig. 184). Setae



FIGS. 180–183. *Macrocheles hirsutissima* (Berlese), female. Fig. 180, dorsal shield. Fig. 181, ventral shields. Fig. 182, chelicera. Fig. 183, tarsus II.



FIGS. 184–187. *Macrocheles pegazzanae* sp. nov., female. Fig. 184, dorsal shield. Fig. 185, ventral shields. Fig. 186, chelicera. Fig. 187, tarsus II.

r1, i4, i5, z2, z3, J2 and J3 simple, remaining setae pilose in their distal halves. Verticals, i1, separated by twice the diameter of their bases.

Sternal shield strongly granular. The structural lines are punctate and inconspicuous (Text-fig. 185). Genital shield broad, shallow, and truncate posteriorly. Ventri-anal shield (240–425μ long × 268–360μ wide) ornamented with incomplete punctate lines and bearing nine simple setae.

The chelicera is shown in Text-fig. 186. The brush-like process of the synarthrodial membrane is short. Six rows of deutosternal teeth.

Genu IV with seven setae, all of which are strongly pilose distally. Tarsus II (Text-fig. 187) 260μ, tibia II 185μ.

MALE. Unknown.

LOCALITIES. The holotype female (1961.7.14.248) and one paratype (1961.7.14.249) on *Phanaeus bellicosus* Oliv. in the Nevinson collection (1918–14) from Sta. Catherina, Brazil; and one paratype (1961.7.14.250) on *Phanaeus dardanus* McLeay from the Moraballi Creek, Essequibo River, British Guiana, collected by the Oxford University Expedition (1929–485).

This species is named after Dr. F. Pegazzano.

Macrocheles spectandus Berlese, 1918

Macrocheles (*Coprholaspis*) *spectandus* Berlese, A., 1918, *Redia* **13** : 151.

FEMALE. Dorsal shield (1,100–1,200μ long × 775–950μ wide) pear-shaped, granular, and almost devoid of ornamentation, and bearing 28 pairs of setae (Text-fig. 188). Setae i4, i5, z2, z3, J2, J3 and J5 simple and short (minimum 27μ). The remaining setae are long (maximum 160μ), slender and sparsely pilose in their distal halves.

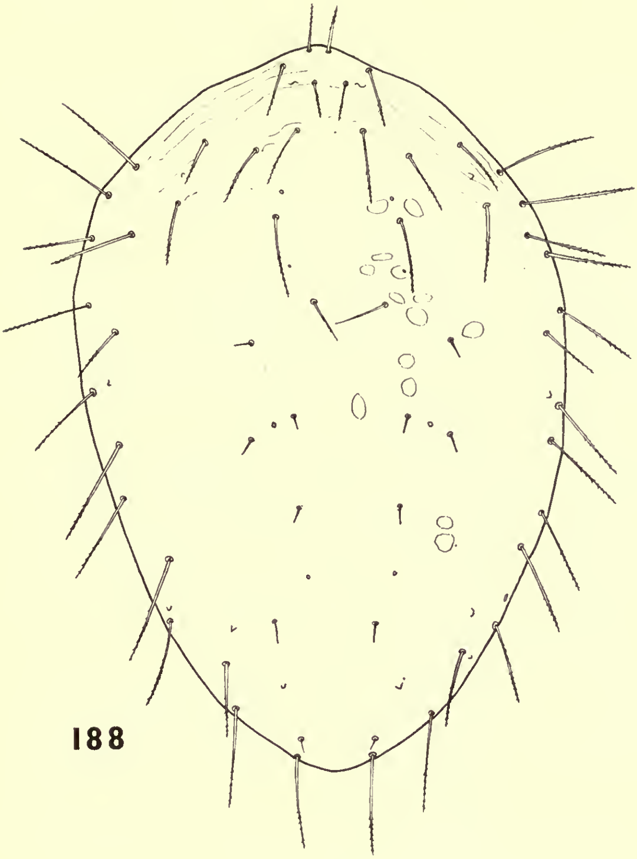
Sternal shield granular, narrow, without ornamentation, strongly concave on all four sides and bearing three pairs of setae which are pilose distally (Text-fig. 189). Genital shield granular, semicircular posteriorly, genital setae pilose distally. Ventri-anal shield (435μ long × 289μ wide) granular, long and tapering, slightly concave laterally. The three anal setae are simple, and the six pre-anal are pilose distally. All setae on the interscutal membrane are pilose distally.

The chelicera is shown in Text-fig. 190. Brush-like process of the synarthrodial membrane less than half the length of the movable digit. Seven rows of deutosternal teeth, the middle three rows being close together. Tectum, Text-fig. 191.

Genu IV with six stout setae, sparsely pilose in their distal two-thirds. Tarsus II with three distal spurs similar to those of *Pachylaelaps* and *Pachyseius* (PACHYLAELAPTIDAE).

MALE. Unknown.

DISTRIBUTION. Berlese (1918) recorded this species from *Eudinopus dytiscoides* Schreib. at Alto Pencosa, San Louis, Argentina. The Museum collections contain nine females from *Eudinopus dytiscoides*, collected by G. E. Bryant (1919–147) at Villa Valeria, Argentina.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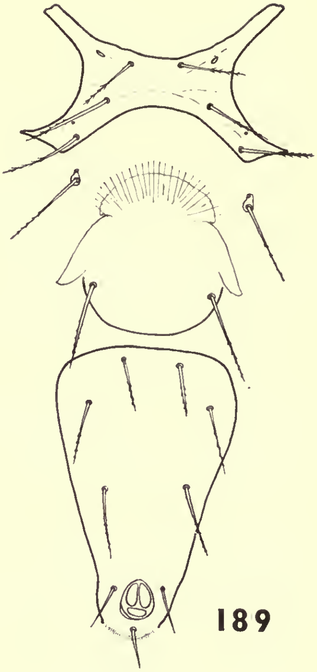
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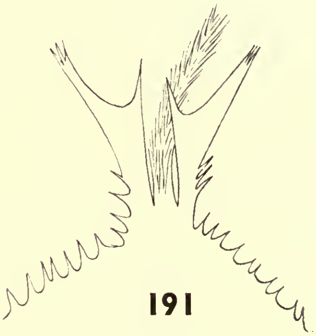
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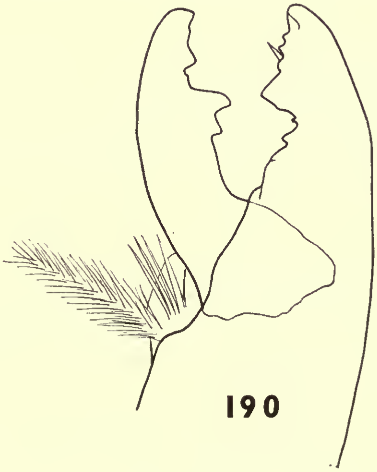
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FIGS. 188–191. *Macrocheles spectandus* Berlese, female. Fig. 188, dorsal shield. Fig. 189, ventral shields. Fig. 190, chelicera. Fig. 191, tectum.

ALPHABETICAL LIST OF COPRID BEETLES WITH ASSOCIATED MITES

Anomiopsis bilobum Burm.	*M. inornatus* sp. nov. (p. 348)
Anomiopsis heteroclytum Blanch.	*M. inornatus* sp. nov. (p. 348)
Canthon principalis Burm.	*M. boxi* sp. nov. (p. 338)
Chalcopsis hesperus Oliv.	*M. austroamericanus* sp. nov. (p. 389)
Circellium bacchus Fabr.	*M. distanti* sp. nov. (p. 348), *M. marshalli* sp. nov. (p. 354)
Deltochilum lobipes Bates	*M. scapularis* sp. nov. (p. 385), *M. grandis* sp. nov. (p. 382), *M. bacchusi* (p. 335)
Deltochilum orbiculare Lansb.	*M. floridanus* sp. nov. (p. 382)
Eudinopus dytiscoides Schreib.	*M. spectandus* Berl. (p. 398) *M. argentinus* sp. nov. (p. 332)
Eurysternus calligrammus Dalm.	*M. bryanti* sp. nov. (p. 338)
Eurysternus claudicans Kirsch	*M. filipponii* sp. nov. (p. 392)
Eurysternus deplanatus Germar	*M. browningi* sp. nov. (p. 338)
Gymnopleurus azureus Fabr.	*M. vernalis* Berl. (p. 375), *M. rhodesi* sp. nov. (p. 365)
Gymnopleurus caffer Fåhr.	*M. vernalis* Berl.. (p. 375)
Gymnopleurus maculosus McLeay	*M. malabaricus* sp. nov. (p. 354)
Gymnopleurus maurus Sharp	*M. baramensis* sp. nov. (p. 335)
Gymnopleurus sinuatus Oliv	*M. japonicus* sp. nov. (p. 351)
Gymnopleurus unicolor Fåhr	*M. vernalis Berl.* (p. 375), *M. transversus* sp. nov. (p. 375), *M. rykei* sp. nov. (p. 369)
Macroderes greeni Kirby	*M. bacchusi* sp. nov. (p. 335)
Megathope argentina Gillet	*M. nevinsoni* sp. nov. (p. 361)
Mnematium marginatum Péring	*M. longisetis* sp. nov. (p. 351)
Mnematium ritchiei McLeay	*M. pyriformis* sp. nov. (p. 365)
Ontherus sulcator Fabr.	*M. austroamericanus* sp. nov. (p. 389)
Phanaeus amethystinus Harold	*M. amygdaligera* Berl. (p. 378)
Phanaeus amythaon Har.	*M. dimidiatus* Berl. (p. 344)
Phanaeus bellicosus Ol.	*M. braziliensis* sp. nov. (p. 391), *M. pegazzanae* sp. nov. (p. 395)
Phanaeus bonariensis Gory	*M. cognatus* Berl. (p. 344), *M. amygdaligera* Berl. (p. 378), *M. bregetovae* sp. nov. (p. 392)
Phanaeus carnifex L.	*M. dimidiatus* Berl. (p. 344)
Phanaeus dardanus McLeay	*M. pegazzanae* sp. nov. (p. 395)
Phanaeus ensifer Germ.	*M. amygdaligera* Berl. (p. 378), *M. dimidiatus* Berl. (p. 344)
Phanaeus faunus Fabr.	*M. amygdaligera* Berl. (p. 378), *M. dimidiatus* Berl. (p. 344)
Phanaeus horus Waterh.	*M. amygdaligera* Berl. (p. 378)
Phanaeus igneus McLeay	*M. amygdaligera* Berl. (p. 378)
Phanaeus imperator Chevr.	*M. cognatus* Berl. (p. 344), *M. amygdaligera* Berl. (p. 341), *M. carteri* sp. nov. (p. 341), *M. austroamericanus* sp. nov. (p. 389)
Phanaeus kirbyi Vigors	*M. austroamericanus* sp. nov. (p. 389)
Phanaeus lancifer L.	*M. hirsutissima* (Berl.) (p. 395), *M. amygdaligera* (Berl.) (p. 378), *M. cognatus* Berl. (p. 344)
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Phanaeus palaeno Blanch.	*M. amygdaligera* Berl. (p. 378)
Phanaeus palliatus Sturm	*M. mexicanus* sp. nov. (p. 358)
Phanaeus scintillans Bates	*M. austroamericanus* sp. nov. (p. 389)
Phanaeus splendidulus Fabr.	*M. phanaei* Berl. (p. 385), *M. dimidiatus* Berl. (p. 344), *M. dubius* sp. nov. (p. 381)

Phanaeus sulcatus Drury	*M. amygdaligera* Berl. (p. 378)
Phanaeus telamon Erichs.	*M. amygdaligera* Berl. (p. 378), *M. austroamericanus* sp. nov. (p. 389), *M. telamoni* sp. nov. (p. 372), *M. turki* sp. nov. (p. 386)
Phanaeus wagneri Har.	*M. bregetovae* sp. nov. (p. 392)
Pinotus carolinus L	*M. filipponii* sp. nov. (p. 392), *M. bregetovae* sp. nov. (p. 392), *M. verticalis* sp. nov. (p. 378)
Scarabaeus bonellii McLeay	*M. rykei* sp. nov. (p. 369), *M. distanti* sp. nov. (p. 348)
Scarabaeus brahminus Cast.	*M. krantzi* sp. nov. (p. 351), *M. nevernalis* sp. nov. (p. 361)
Scarabaeus carinatus Gebler	*M. vernalis* (Berl.) (p. 375)
Scarabaeus cristatus Fabr.	*M. vernalis* (Berl.) (p. 375)
Scarabaeus cuvieri McLeay	*M. natalensis* sp. nov. (p. 358)
Scarabaeus erichsoni Harold	*M. ceylonicus* sp. nov. (p. 341), *M. krantzi* sp. nov. (p. 351)
Scarabaeus gangeticus Cast.	*M. vernalis* (Berl.) (p. 375), *M. thomasetti* sp. nov. (p. 372)
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Scarabaeus prodigiosus Er.	*M. abbreviatus* Berl. (p. 332)
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NATURAL HISTORY

SUMMARY

The external morphology and classification of the insecticolous species of *Macrocheles* are discussed with particular reference to 46 species collected from coprid beetles in the Collections of the British Museum (Natural History). These species, of which 38 are considered new, are described and figured.

REFERENCES

BERLESE, A. 1903. Acari nuovi. *Redia* **1** : 258–280.

—— 1910. Lista di nuove specie e nuovi generi di Acari. *Redia* **6** : 242–271.

—— 1918. Centuria quarta di Acari nuovi. *Redia* **13** : 115–192.

Evans, G. O. 1956. On the classification of the family Macrochelidae with particular reference to the subfamily Parholaspinae (Acarina—Mesostigmata). *Proc. zool. Soc. Lond.* **127** : 345–377.

Evans, G. O. & Browning, E. 1956. British mites of the subfamily Macrochelinae Trägårdh (Gamasina—Macrochelidae). *Bull. Brit. Mus. (nat. Hist.), Zool.* **4** : 1–55.

FILIPPONI, A. & PEGAZZANO, F. 1960. Acari del genere *Glyptholaspis* nom. nov. pro *Macrocheles* (*Macrocheles*) Berl. 1918 (Mesostigmata, Macrochelidae). *Redia* **45** : 133–171.

HIRSCHMANN, W. 1917. Acarologie. Gangsystematik der Parasitiformes. Teil 1—Rumpfbehaarung und Rückenflächen. Schriften für vergleichende Milbenkunde, Fürth/Bay.

KRANTZ, G. W. 1962. A review of the genera of the family Macrochelidae Vitzthum 1930 (Acarina : Mesostigmata). *Acarologia* **4** : 143–173.

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